Alarm Calls and Information Use in the New Holland Honeyeater

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Predation is a major source of mortality, resulting in strong selection on strategies to avoid being captured. Individuals have access to multiple sources of information on predation risk: they can detect danger directly themselves, and they can attend to behavioural cues or warning signals produced by others. Rapid responses are vital when hunted by aerial predators in particular, as split-second decisions can mean the difference between life and death. I studied New Holland honeyeaters, *Phylidonyris novaehollandiae*, as a model system to examine how alarm calls encode information about danger and to understand how this information is used by receivers. In Chapter 2, observational data showed that these honeyeaters produce multi-element, aerial alarm calls in response to flying threats. Male honeyeaters had more opportunities to detect threats than did females and showed a greater propensity to alarm call when presented with gliding model predators. In Chapter 3, a combination of observational data and model presentations demonstrated that aerial alarm calls encode urgency in both the number of elements, with more dangerous threats receiving more elements, and the acoustic structure of the first element. Playback presentations of alarm calls and video recordings to measure responses revealed that honeyeaters made extremely fast decisions about fleeing to cover based on the acoustic structure of the first alarm element, while the number of elements determined for how long they hid. These two chapters demonstrate that receivers have rapid access to detailed information about the type and degree of danger from conspecific alarm calls. In Chapter 4, I investigated how birds integrate personal information about danger with social information from alarm calls. Perched birds were faster to detect model predators than feeding birds, suggesting that they have greater access to personal information. Consistent with this, perched birds were less likely to flee to cover in response to alarm playbacks than foraging birds. Birds also fled less in response to less urgent social information, such as playbacks of more distant alarm calls, and less relevant social information, in the form of calls from another species with overlapping but not identical

threats. In Chapter 5, I tested how honeyeaters value social information about danger derived from single versus multiple sources, both within and across species. Birds paid attention to the number of independent signallers when assessing information from both conspecifics and heterospecifics, responding more strongly to playbacks of alarm calls from two sources than a single source, but they also moderated their responses according to signal relevance. Together, these results show that birds make flexible decisions about danger by integrating information from multiple sources and assessing its quality, allowing them to mitigate the costs of fleeing to false, or irrelevant, alarms while taking advantage of the multitude of information provided by the prey community's neighbourhood watch.

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Preface

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit of 60, 000 words for the Biology Degree Committee.

Thesis Summary

Predation is a major source of mortality, resulting in strong selection on strategies to avoid being captured. Individuals have access to multiple sources of information on predation risk: they can detect danger directly themselves, and they can attend to behavioural cues or warning signals produced by others. Rapid responses are vital when hunted by aerial predators in particular, as split-second decisions can mean the difference between life and death. I studied New Holland honeyeaters, *Phylidonyris novaehollandiae*, as a model system to examine how alarm calls encode information about danger and to understand how this information is used by receivers. In Chapter 2, observational data showed that these honeyeaters produce multi-element, aerial alarm calls in response to flying threats. Male honeyeaters had more opportunities to detect threats than did females and showed a greater propensity to alarm call when presented with gliding model predators. In Chapter 3, a combination of observational data and model presentations demonstrated that aerial alarm calls encode urgency in both the number of elements, with more dangerous threats receiving more elements, and the acoustic structure of the first element. Playback presentations of alarm calls and video recordings to measure responses revealed that honeyeaters made extremely fast decisions about fleeing to cover based on the acoustic structure of the first alarm element, while the number of elements determined for how long they hid. These two chapters demonstrate that receivers have rapid access to detailed information about the type and degree of danger from conspecific alarm calls. In Chapter 4, I investigated how birds integrate personal information about danger with social information from alarm calls. Perched birds were faster to detect model predators than feeding birds, suggesting that they have greater access to personal information. Consistent with this, perched birds were less likely to flee to cover in response to alarm playbacks than foraging birds. Birds also fled less in response to less urgent social information, such as playbacks of more distant alarm calls, and less relevant social information, in the form of calls from another species with overlapping but not identical

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First and foremost, I would like to express my boundless gratitude to my two supervisors, Nick Davies and Rob Magrath, without whom this thesis would not exist. It still astonishes me that I have had the privilege to work under Nick's tutelage. His influence on my life began long before he knew my name when I was an eager undergrad enthralled by his behavioural ecology lectures and scribblings upon the overhead projector. Those fascinating lectures were integral in forming my research interests today. Nick has proved to be the most wonderful supervisor, giving me the freedom to investigate whatever questions tickled my curiosity and supporting my research with a great enthusiasm that never failed to lift my spirits on days when I had begun to doubt. His interest in my work always helped to remind me why it was interesting at times when honeyeaters seemed so far away from my desk in Cambridge. He has suffered patiently through so many drafts of this thesis and his ability to see the forest, rather than the trees, has immeasurably improved it. It has been lovely to tell stories of my honeyeaters to someone who shares my appreciation for quiet observations of wild birds. I am incredibly grateful that I have had the chance to work with Nick and benefit in so many ways from his sage guidance.

I daresay that when Rob agreed to help Andy Radford supervise my masters project, he had little notion that, over half a decade later, he would still be fending off my questions. I will forever be indebted to Rob for agreeing not once but twice to take me on. He has shaped me into the researcher I am today, with his incredible generosity and willingness to share his knowledge of acoustics and the birds of the botanic gardens. I have learnt so much about experimental design and acoustic analysis (and more than I ever wished to know about calibration) from Rob, and he has invested far more time in developing my skills than I deserve. Our discussions of possible experiments, experimental results or whatever exciting thing I had seen in the gardens that day were one of the highlights of working in Australia. His willingness to open his door to my (apparently recognisable) knock to answer yet

another “quick” question that would inevitably transform into an hour of excited babble on the subject of my amazing honeyeaters is nothing short of heroic. In addition to all the advice he gave me for experiments, I am also thankful for the many early mornings he spent with me catching and banding the honeyeaters, which made this research possible. I am extremely glad that I have had so many opportunities to work with Rob and to learn from him over the years.

I would also like to thank my two advisors, Claire Spottiswoode and Rufus Johnstone, for their annual comments and feedback on my research. It was great to have the chance to discuss my thesis with them and benefit from their insights and different perspectives on familiar topics.

This research was funded by a studentship from the Natural Environment Research Council, and I am very appreciative of their financial support that made it possible for me to embark upon this PhD.

I am grateful to the members of the Behavioural Ecology Group in Cambridge and Magrath Lab in Canberra with whom I shared many interesting discussions on topics ranging from whose honeyeater species is better (mine, obviously) to fantasy books, from fieldwork failures to thesis formatting. The model presentation experiment in Chapter 4 would not have been possible without the help of Chaminda Ratnayake, who came out to throw the models early each morning despite a family crisis. Particular thanks must go to Branislav Igic, Carmen Panayi and Elisa Dierickx. Brani took on the role of my academic older sibling and was always available to answer whatever panicked question came his way (usually about stats), even when we were cities and oceans apart. I will never forget our chats in my office or the courtyard, conducted over the heavenly mangoes or naartjies that he had provided, during which we laughed far more than any two people probably should. Carmen and Elisa made long days of writing up in Cambridge so much more bearable, even after they’d both finished up their PhDs and taken up other jobs. From lunches to dinners to movies, their friendship has brightened up even the dreariest of days. I owe Elisa both apologies and gratitude for the desk swap that meant I could type away on the subject of honeyeaters without interruption from corridor

distractions. And, of course, no amount of writing fatigue could resist the uplifting effects of Carmen's animal menagerie. Loki, in particular, has been the cutest and cuddliest antidote to thesis blues.

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I would like to thank the staff of the Australian National Botanic Gardens, who allowed me to work in their wonderful gardens and gave me permission to deviate from the paths when in search of birds. Unfortunately, I failed to capture the gardeners' many spontaneous dances that were performed in front of my video camera, as the camera was sadly never running at such times. I also apologise to all the visitors I scared with my playback outfit and to those who will never learn what the strange, human-like statue was supposed to signify.

I am grateful to my proofreading minions – Mum, Dad, Kate, Eugénie, Nick, Carmen, Lauren and Josie - who stepped in at the eleventh hour (well, considerably closer to midnight) to read through drafts. Subsequent last-minute alterations may have undone some of their good work on the multitude of tables, figures and references. Particular credit must go to Josie Parker, who read through a draft despite having malaria, which is remarkable dedication.

And, of course, to my family, each of whom has supported me throughout the course of my PhD in their own way.

Kate has been through this all before and could give me encouragement and advice on assorted aspects of the PhD process. The fact that Kate studies communication in humans, rather than in birds, meant she was happy to join me in thought-provoking discussions about communication and

whether or not humans have alarm calls. She also read through a lot of drafts at the last minute, for which I am most grateful.

Eugénie has been the architect of many fabulous adventures in the UK, without which my life would been infinitely less exciting (even though they occasionally came close to ending it). She and Rob were kind enough to make their home mine for so many weekends over the years, which has been wonderful, and I have had tremendous fun in their company. She is singlehandedly responsible for all the meals I have consumed over the last few months that have consisted of more than just cereal or a theoretically nutritionally balanced shake, so she can get the credit for my continued existence.

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My parents have kindly supported me through a very lengthy education, allowing me to build castles in the air and helping me to construct the foundations beneath them. It was my mother who gave me the book that made an 11-year-old me decide to become a zoologist, changing my life forever. It was my father who made it possible for that dream to be realised. Thanks go to my dad for bringing me home to see everyone each Christmas and for enabling me to come on the family holidays around America, as well as for regular deliveries of delicious fruit and unexpected phone calls to check on me as he drove to work. My mother was the first to read every chapter of this thesis and her feedback has shaped each one of them. As she read so many essays from my undergraduate and both theses from my postgraduate degrees, I think she deserves an honorary degree in biology at this point. However, my eternal gratitude will have to suffice.

But the final thanks must go to the birds themselves, the stars of this thesis. They were only meant to be the focus of a single chapter in the original conception of my PhD, but it did not take long for it to become clear that they were far too fascinating in their own right to be relegated to a supporting role. I am glad that I had worked on half a dozen other species of birds before them, so that I could truly appreciate quite how wonderful New Holland honeyeaters are. It has been a privilege to work on these bright and busy characters, who have greatly enriched my life. They led me to almost every exciting predator encounter I had, both in the botanic gardens and on hikes around Australia. While individuals may be reduced to binary fleeing scores and random effects in the thesis, I treasure each of their stories and all the interactions and details I observed that are beyond the remit of this thesis. Particular mentions must be made of the dashingly handsome WYY (so handsome that he gets to feature on two chapter covers), the ever-reliable WNR, the tragic tale of RMR, the once infuriating but now much-loved RBD (whose rare moment of perching is now captured for posterity on the bottom of every page of this thesis), the scaredy-cat RON, the sweet romance of DMB and WNY, and the incessant calling of little BOB. This list could comfortably continue on to describe every bird I worked on, all of which are very dear to me, and I am hardly the first person to have fallen in love with these birds. A Mr Alwyn Pepper of Scaraborough described his captive honeyeaters in similarly glowing terms in 1972:

> "the New Holland honeyeater (*Phylidonyris novaehollandiae*) is a very handsome bird strikingly coloured black, white and yellow… To be able to observe these lovely birds at close quarters is indeed a fascinating and rewarding pastime. They are so vastly different, in all respects, from the usual run of everyday finches, parrots, etc… Watch them gracefully and effortlessly twist and turn in mid air as they hawk for insects. Watch their fantastic flash of gold as they flit from flower to flower to cling precariously whilst probing their long curved bills deep into colourful blossoms in their never ending search for nectar."

Although more recent descriptions have slanderously labelled New Holland honeyeaters as “pugnacious”, they are, as Mr Pepper says, fascinating and brilliant little birds. I have truly loved doing my PhD on them, and, sad though it will be to submit my thesis and watch this part of my life come to an end, it will not come close to how hard it was to say goodbye to these bird and walk out of the gardens one final time to the distant sound of WRB warning all of us that the damned butcherbird was back again.

Chapter 1

General Introduction

A hunting hawk explodes from the canopy, yellow-eyed death on silent wings. It hurtles from the sky at astonishing speed towards the bustling tangle of pink flowers and intently feeding birds. But a staccato warning sounds from above: loud, clear, rapid notes fired through the lively chatter. The pink bush trembles beneath a dozen flights of fear and desperate departures. And the hawk rises up, empty-taloned, a chorus of alarm calls stretching long behind it like a late afternoon shadow.

Predation is a major source of mortality. As such, there is strong selection on strategies to avoid being captured, ranging from the evolution of cryptic colouration to minimise the chances of detection, to group living to reduce the risk of being the one that is eaten (Caro, 2005). For animals that rely on behavioural responses to evade danger, such as freezing or fleeing, information about predators is vital for survival, and knowledge about the presence of a predator could mean the difference between life and death. Although individuals can detect predators themselves through their personal information, they can also use social information derived from the cues or warning signals from other individuals. So, while a bird that has its head buried inside a flower may not notice the approach of a predator, an alarm call from one of its neighbours could save its life.

In this thesis, I will address the transfer of information about danger in avian communities, by considering how individuals communicate about predators and how receivers make use of the information available to them. Alarm calls make an ideal system for understanding communication: they tend to be structurally distinctive vocalisations produced in specific contexts that have clear survival implications, they often prompt unambiguous responses in receivers, and they are produced by a wide range of species (Zuberbühler, 2009). These calls have therefore been studied extensively as model systems for understanding signal design (Marler, 1955, 1957), the meaning of signals (Seyfarth et al., 1980) and the evolution of signaling (Charnov & Krebs, 1975; Maynard Smith, 1965; Trivers, 1971).

Despite considerable research into alarm calling, there are still aspects of this behaviour about which we know relatively little. For example, although alarm signals often require urgent responses

from receivers, our knowledge is largely confined to understanding how the signals convey that urgency and not how rapidly receivers can extract the necessary information from the calls. Given the speed of attacking hawks, receivers will need to make split-second decisions in order to evade capture (Goslow, 1971; Kane et al., 2015; Malmiga et al., 2014; Zoratto et al., 2010). More generally, with the high stakes associated with predator detection, it is surprising that alarm calling has garnered little attention in the context of information use. Reviews on information rarely include much reference to alarm signals (e.g. Bonnie & Earley, 2007; Dall et al., 2005; Danchin, 2004; Rieucau & Giraldeau, 2011; cf. Schmidt et al., 2010). Yet alarm calls are an excellent model for studying information use, as individuals are likely to have access to personal information on the presence of a predator as well as information from alarm calls, potentially given by several callers or species. They consequently provide an opportunity to examine how individuals value and integrate information derived from multiple sources in a deadly context.

In this introductory chapter, I review the literature on the different types of information about danger available to individuals, with particular focus on alarm calls.

1.1 PERSONAL INFORMATION ABOUT DANGER

In order to successfully escape from predators, individuals first must be able to detect threats. Early detection can increase the chances of escaping and reduce the risk of being targeted, while being the one to notice the predator could ensure that the detector can also be amongst the first to escape (Clutton-Brock et al., 1999; Cresswell, 1993; Griesser & Ekman, 2005). Animals have therefore evolved a variety of ways of detecting predators, taking advantage of a range of sensory modalities.

Visual detection

Animals across a wide range of taxa are able to visually identify predators (e.g. Carlson et al., 2017; Elmasri et al., 2012; Lohrey et al., 2009; McCormick & Manassa, 2008; Narayan et al., 2013; Nováková et al., 2017). The salient features that facilitate visual recognition of predators vary across species and predators. For example, visual looming is an important cue for fiddler crabs, *Uca vomeris*,

hermit crabs, *Coenobita clypeatus*, jack dragons, *Amphibolurus muricatus*, and mice, *Mus musculus* (Carlile et al., 2006; Hemmi, 2005; Shragai et al., 2017; Smolka et al., 2011; Yilmaz & Meister, 2013), whereas the response of bonnet macaques, *Macaca radiata*, to leopard, *Panthera pardus*, models is dependent on the presence of spots and the orientation of the model (Coss et al., 2005; Coss & Ramakrishnan, 2000), and reef fish identify predatory fish by their mouth size (Karplus et al., 1982). Given the prevalence of visual recognition of predators, one of the best studied strategies of predator detection is vigilance, where animals raise their heads to visually scan the environment (Caro, 2005). Individuals that are engaged in vigilance are faster to spot predators than non-vigilant individuals in fish (Krause & Godin, 1996), birds (Devereux et al., 2006; Hilton et al., 1999; Whittingham et al., 2004) and mammals (Robinson, 1981).

Individuals that visually detect predators can do more than simply respond to their presence: they can adjust their responses according to the type of predator detected or its current behaviour. Slimy sculpins, *Cottus cognatus*, and domestic fowl, *Gallus gallus domesticus*, alter their anti-predator behaviour according to the size of the predator they face (Chivers et al., 2001; Palleroni et al., 2005). Several mammals and birds show different behavioural and vocal responses to ground and aerial predators, approaching and harassing ground predators, and fleeing or freezing when faced with a flying raptor (Evans et al., 1993; Graw & Manser, 2007; Macedonia & Evans, 1993; MacWhirter, 1992; Townsend & Manser, 2013). Red knots, *Calidris canutus*, spend less time foraging and more time vigilant when presented with a gliding, rather than perched, sparrowhawk, *Accipiter nisus*, (Mathot et al., 2009) and blue tits, *Cyanistes caeruleus*, reduce feeding if a perched sparrowhawk model moves its head instead of remaining immobile (Carlson et al., 2017). In species from black-tailed deer, *Odocoileus hemionus*, to fiddler crabs, individuals are more fearful of predators that approach more directly or more rapidly (Bateman & Fleming, 2011; Hemmi, 2005; Scarano & Tomsic, 2014; Sreekar & Quader, 2013; Stankowich & Coss, 2006). Birds can even assess the direction in which predators are looking, regardless of whether the predator is another bird, a reptile or a mammal, and reduce feeding when the predators are facing them (Book & Freeberg, 2015; Cantwell et al., 2016; Carter et al., 2008;

Freeberg et al., 2014). They also change their escape behaviour according to the steepness of the angle at which the predator is approaching and whether they are in direct line of attack (Lima & Bednekoff, 2011; Lind et al., 2002, 2003). Visual detection of predators thus provides richly detailed information on predator presence, proximity and behaviour.

Acoustic detection

In addition to visually scanning the environment, individuals can also take advantage of acoustic cues to detect predators. This is likely to be particularly important for animals that have limited access to visual information about their environment, such as nocturnal species. Bat predation using echolocation represents an important selection pressure on the hearing of insects (Hoy, 1992), so it is unsurprising that night-flying insects show strong responses to the calls of hunting bats. Green lacewings, *Chrysopa carnea*, in flight will fold their wings when presented with a playback of a bat call in an attempt to drop below the bat's sonar system, but if a dropping lacewing is then presented with the terminal buzz of a bat honing in on its prey, it will open its wings again to ensure an unpredictable trajectory (Miller & Olesen, 1979). Similar responses have been found in eared moths, which gently turn in response to low intensity bat calls and engage in random flight following high intensity calls to reduce the risk of capture (Yager, 2012).

Predators that do not use sound to hunt can still reveal their presence through the sounds they make. There is indirect evidence that animals engage in general acoustic monitoring of their environments: birds increase their investment in visual vigilance when presented with high levels of background noise (Klett-Mingo et al., 2016; Quinn et al., 2006), and ruminants pause more often when chewing, a noisy activity, at night time (Blanchard & Fritz, 2007; Lynch et al., 2015). This suggests that animals value potential acoustic information on danger, and studies show that animals do attend to acoustic cues of predator presence. White-browed scrubwren, *Sericornis frontalis*, nestlings suppress calling when they hear the sound of a nest predator walking nearby, reducing the likelihood of being detected (Haff & Magrath, 2010). Insects are not only sensitive to bat calls, as noctuid moths and nymphalid butterflies take evasive action when they hear the wing beats of birds (Fournier et al.,

2013). Furthermore, prey species can pay attention to the social vocalisations of predators to assess predation risk (reviewed in Blumstein et al., 2008). For example, wolf spiders, *Schizocosa ocreata*, stop moving after hearing the calls of predatory birds (Lohrey et al., 2009), while impalas, *Aepyceros melampus*, increase vigilance and decrease foraging following playbacks of lion, *Panthera leo*, roars (Favreau et al., 2013). Animals can acquire detailed information on the type of predator from their calls alone: black-capped chickadees, *Poecile atricapillus*, respond more strongly to the calls of smaller raptors, which represent a more dangerous threat (Billings et al., 2015), and red-tailed sportive lemurs, *Lepilemur ruficaudatus*, scan up to hawk calls and look down when they hear fossa, *Cyptoprocta ferox*, calls, recognising the likely location of the threat (Fichtel, 2007). In fact, harbor seals, *Phoca vitulina*, are able to discriminate probable predators from non-predators within a species, as they only leave the water when presented with the vocalisations of transient killer whales, *Orcinus orca*, which hunt seals, but remain in the water when they hear the sounds of resident killer whales that focus on hunting fish (Deecke et al., 2002).

Chemical detection

While sight and sound are transient cues that indicate current predator presence, chemical cues of danger can persist over time and enable individuals to assess the presence of predators without directly interacting with them. There is a considerable volume of literature demonstrating that mammals respond to mammalian predator odours (reviewed in Apfelbach et al., 2005). Typical short-term responses include changes in space use, such as American beavers, *Castor canadensis*, avoiding trails treated with wolf, *Canis lupus*, urine (Severud et al., 2011), reduction in feeding, for instance kangaroos, *Macropus fuliginosus*, foraging less on food associated with dingo, *Canis lupus dingo*, urine (Parsons & Blumstein, 2010), and heightened vigilance, such as roe deer, *Capreolus capreolus*, spending more time with their heads raised in the presence of lynx, *Lynx lynx*, urine (Eccard et al., 2017). Chemical detection of predators is not unique to mammals, however. House finches, *Carpodacus mexicanus*, great tits, *Parus major*, and blue tits show spatial avoidance when exposed to the smell of predators (Amo et al., 2011, 2015, 2017), and domestic fowl, *Gallus gallus domesticus*,

feed less and are more vigilant when exposed to predator faeces (Zidar & Løvlie, 2012). Bees avoid crab spider, *Synaema globosum*, mantis, *Tenodera sinensis*, or predatory ant, *Oecophylla smaragdina*, odours (Bray & Nieh, 2014; Li et al., 2014; Reader et al., 2006). Scent is particularly important in aquatic environments, where visibility can be low. As such, many aquatic species display anti-predator behaviour when presented with predator odours, known as kairomones (for reviews, see Ferrari et al., 2010; Mitchell et al., 2017).

Animals that detect chemical cues can gain additional information about potential predators from the odours. As scents linger in an area, individuals can assess the recency of the predator's visit. Rats, *Rattus fuscipes*, avoid areas laced with dog, *Canis lupus familiaris*, urine but do so less as the urine ages (Bytheway et al., 2013). Similarly, meerkats, *Suricata suricatta*, show higher levels of vigilance and greater recruitment to fresh urine compared to older urine (Zöttl et al., 2013). Nesting ducks and fathead minnows, *Pimephales promelas*, can assess predator density from chemical cues (Eichholz et al., 2012; Ferrari et al., 2006). While velvet geckos, *Oedure lesueurii*, have a generalised anti-predator response to all snake odours (Webb et al., 2009), Cape ground squirrels, *Xerus inauris*, increase their performance of snake-harassment behaviours to odours derived from venomous, rather than non-venomous, snakes (Phillips & Waterman, 2013). Wolf spiders and fathead minnows show graded responses to predator odours, according to the size of the predator (Kusch et al., 2004; Persons & Rypstra, 2001). Thus, individuals with direct access to cues of predator presence can make assessments about the degree of risk, even when using a long-lasting cue.

Close-range detection

Animals that fail to perceive predators at a distance may still be able to detect them at close range and avoid capture. *Heterozus rotundifrons* crabs adopt an immobile posture when touched or when either chemical or visual stimuli cross a threshold intensity, relying on their hard shell to protect them (Hazlett & McLay, 2005). Similarly, wolf spiders freeze when exposed to a simulated bird beak tap (Lohrey et al., 2009). Several insects have specialised leg or thoracic hairs which allow them to detect air movements in close proximity and are fine-tuned to movements caused by predators

(Camhi et al., 1978; Dupuy et al., 2011; Magal et al., 2006; Tautz & Markl, 1978). These insects need to show very fast escape maneouvres to avoid predators: praying mantises only detect approaching bats through air movements about 75 ms before impact (Triblehorn & Yager, 2006). While this is unlikely to be enough time to avoid the predator entirely, insects could alter their trajectory sufficiently to increase the likelihood of mishandling by the predator (Triblehorn & Yager, 2006). Cockroaches, *Periplaneta americana*, are reported to successfully evade capture using wind detection alone 55% of the time, but locusts only managed to escape about 20% of the time, suggesting that this is a last-ditch defence when earlier detection mechanisms have failed (Camhi et al., 1978; Santer et al., 2012). Crayfish, *Procambarus clarkii*, on the other hand, are able to escape or break free during 80% of predator encounters by performing tail-flips, which are triggered by touch (Herberholz, 2004). However, the size discrepancy between predator and prey is considerably smaller in this instance.

Some species are sensitive to vibrations through the substrate instead, facilitating detection and evasion over relatively short distances. Termites, *Coptotermes acinaciformis*, detect predatory ants, *Iridomyrmex purpureus*, by the vibrations they cause when walking (Oberst et al., 2017). Red-eyed treefrogs, *Agaychnis callidryas*, show escape-hatching from their eggs if exposed to vibrations caused by approaching egg-predators, and they are sensitive to the specific frequencies associated with predators to avoid premature hatching due to false alarms (Caldwell et al., 2009). *Semiothisa aemulataria* caterpillars can even differentiate between predator types by their substrate-borne vibrations, hanging on a silk thread in response to predatory invertebrates in close proximity and adjusting the thread length according to the specific threat (Castellanos & Barbosa, 2006). So even when relying on short-range detection abilities, some species can extract detailed information from their environments.

1.2 Information from others

Although there are benefits to being the individual that detects the predator (Lingle & Wilson, 2001), it is not possible for animals to be vigilant at all times. Vigilance is at least partially incompatible

with other behaviours; for example, vigilance can reduce food intake (Fortin et al., 2004; Pöysä, 1987), and individuals that are feeding are slower to detect predators, particularly if the foraging task is challenging (Bohórquez-Herrera et al., 2013; Dukas & Kamil, 2000). Feeding is not the only constraint on detection: animals show reduced responsiveness to stimuli when they are sleeping (Czisch et al., 2002; Lima et al., 2005; Livingstone & Hubel, 1981), and social interactions, such as play, aggression and courtship displaying, can all adversely impact an individual's ability to detect oncoming threats (Blumstein, 1998; Cords, 1995; Cowles & Gibson, 2015; Hebets, 2005; Hess et al., 2016; Yee et al., 2013). But animals need not always notice the predator themselves; they can use information derived from other individuals that may have spotted the threat first. This information can take the form of either cues or alarm signals. Signals are stimuli produced by signallers that modify the behaviour of receivers. Cues are also stimuli that can affect the behaviour of others but do so inadvertently. Unlike cues, signals have been acted upon by selection to elicit the change in receiver behaviour, and receivers' responses have also been selected for (Maynard Smith & Harper, 2003).

Conspecific cues

Enhanced predator detection as a result of many eyes looking out for danger is one of the hypotheses for social foraging in animals, and there is evidence that larger groups can detect threats more rapidly (Boland, 2003; Ebensperger & Wallem, 2002; Kenward, 1978; Lima, 1995; Powell, 1974). Animals are sensitive to changes in conspecific vigilance, which can facilitate collective detection of predators (Pays et al., 2013; Walther, 1969). Sleeping gulls interrupted their sleep to scan more frequently if their neighbours were in a state of alertness, and ringed salamanders, *Ambystoma annulatum*, stopped moving if they saw conspecifics react to a predator's presence (Beauchamp, 2009; Crane et al., 2012). Other aspects of conspecific anti-predator behaviour can inform naïve individuals. Wood crickets, *Nemobius sylvestris*, housed with conspecifics that had been exposed to a predator showed similar hiding behaviour to the knowledgeable individuals, with the behaviour persisting even after the demonstrators had been removed (Coolen et al., 2005a). Individuals can respond to the absence of a cue by attending to subtle postural changes: pigeons, *Columba livia*, only

become alarmed if other individuals take off without demonstrating specific pre-flight behaviours first, the absence of which indicates an escape flight (Davis, 1975). Similarly, a sudden silence indicating the cessation of movement or calling can be perceived as a cue of danger in rats and frogs (Dapper et al., 2011; Pereira et al., 2012). Animals can also make decisions about the direction of their escape based on the behaviour of conspecifics; for example, starlings, *Sturnus vulgaris*, that have not spotted an approaching predator will adjust their escape trajectory according to the direction of flight of the birds that did detect the threat (Devereux et al., 2008).

Chemical alarm cues, in some cases, can straddle the gap between cues and signals. Over 100 aquatic species across different taxa have chemical alarm cues, released by damage to their skin, that trigger antipredator responses in conspecifics, such as increased use of shelter or avoidance of the area (reviewed in Ferrari et al., 2010). Conspecifics that have access to these alarm cues have enhanced survival due to their antipredator responses, and there is some evidence that the individuals that release the chemicals can gain an advantage by attracting secondary predators, which may disrupt the initial predator's feeding and increase the likelihood of escape (Chivers et al., 1996; Mathis & Smith, 1993). However, the production of the epidermal cells that release these chemical cues is related to exposure to skin pathogens, parasites and UV radiation, not predation, suggesting that the chemicals have not been acted upon by selection for antipredator signaling (Chivers et al., 2007; Wisenden & Chivers, 2006). Chemical cues found in the urine of stressed individuals can alter the behaviour of conspecifics, prompting avoidance, altered exploratory activity, and longer latencies to feed (Boissy et al., 1998; Jordão, 2004; Zulandt Schneider & Moore, 2000). In aquatic species, individuals that attend to chemical cues from conspecifics can adjust the intensity of their responses according to the concentration of chemicals, which can indicate the spatial or temporal proximity to the predation event (Ferrari et al., 2010), and one species can even discriminate between damaged conspecific of different sizes, responding most strongly to cues from those of a similar size (Mirza & Chivers, 2002).

Conspecific alarm calls

Cues from alarmed individuals are not the only source of conspecific information, as many species have evolved alarm signals to warn conspecifics about potential danger (Caro, 2005). Alarm calls are specific vocalisations that are produced in the presence of predators and elicit antipredator behaviour in conspecific receivers (Magrath et al., 2015a). They have fascinated biologists for a long time, providing a model system for the study of signal design, a window into the cognition of other animals, and raising the puzzle as to why animals might signal in the face of danger. Broadly, there are two main types of alarm calls: 1) mobbing alarm calls prompt approach, inspection and harassment of predators that do not pose an immediate threat, and 2) flee alarm calls elicit fleeing or freezing responses to predators that require immediate action.

Evolution of alarm calls

The wide-spread presence of alarm calling amongst vertebrates has long presented a challenge for scientists, as calling in the presence of danger seems to be maladaptive (Zuberbühler, 2009). One way in which a signaler might indirectly benefit from producing a warning signal during a predation event is if it preferentially calls in the presence of kin. For example, female Belding's ground squirrels, *Spermophilus beldingii*, and black-tailed prairie dogs, *Cynomys ludovicianus*, are more likely to alarm call when they have relatives, either offspring or nondescendant kin, nearby (Hoogland, 1983; Sherman, 1977). The relationship between alarm calling and relative presence can be affected by both the sex of the potential signaler and the type of alarm call: male Siberian jays, *Perisoreus infaustus*, are more likely to give mobbing alarms in the presence of offspring than unrelated immigrants, but they give flee alarm calls regardless of group composition, whereas females are more likely to give flee alarms if their offspring are around (Griesser & Ekman, 2004, 2005).

Invoking kin selection as an explanation for the evolution of alarm calls might not be necessary if individuals receive direct benefits from calling. There is little empirical evidence to suggest that alarm calling is costly, and it may even be beneficial, as several studies have found that predators were less likely to attack individuals, or species, that called (Kareksela et al., 2013; Pavey & Smyth, 1998;

Sherman, 1985). By recruiting other individuals to harass a potential predator, both the caller and receivers might benefit by driving the predator away (Flasskamp, 1994; Pavey & Smyth, 1998; Pettifor, 1990). As observational data suggest larger mobbing groups are more effective at persuading predators to leave than smaller groups, calling may enable the signaler to achieve the desired outcome, which might not have been possible had it acted alone (Flasskamp, 1994; Robinson, 1985). Alternatively, an alarm call might signal to the predator that it has been spotted. For instance, a radio-collared leopard, which is an ambush predator, was found to abandon hunting following detection and alarm calling by groups of monkeys (Zuberbühler et al., 1999). Of course, alarm callers could accrue more than one sort of benefit to offset any potential costs of calling.

Information available from alarm calls

Alarm calls can signal specific types of predators, resulting in the suggestion that these calls may be functionally referential, a necessary precursor to language (Gill & Bierema, 2013; Macedonia & Evans, 1993; Seyfarth & Cheney, 2003; Smith, 2017; Townsend & Manser, 2013). Classic research on vervet monkeys, *Cercopithecus aethiops*, demonstrated that they produce distinct calls for different classes of predator – leopards, eagles and snakes – that are associated with different escape strategies. Furthermore, the monkeys responded appropriately to playbacks of each type of conspecific alarm: they run into trees in response to leopard alarm calls, they scan the sky and run for cover to eagle alarm calls, and they stand bipedally and scan the ground when presented with snake alarm calls (Seyfarth et al., 1980). In several species of birds and mammals, the acoustically distinct flee and mobbing alarm calls signify broad classes of predator, as they are commonly associated with flying and ground predators, respectively (Smith, 2017; Suzuki, 2016). Siberian jays even use specific calls to signal about different predator behaviour as well as to differentiate between predator types (Griesser, 2008, 2009a). More recently, work on Japanese tits, *Parus minor*, showed that playbacks of their snake-specific alarm call result in receivers forming a visual search image of snakes, providing support for the idea that alarm calls are referential (Suzuki, 2018). While research interest in referential alarm communication may be driven by the cognitive and linguistic insights it yields, such

a system has clear advantages for the receivers, which can adopt threat-appropriate escape strategies according to the call type to increase the likelihood of survival (Griesser, 2013; Griesser & Suzuki, 2017).

As well as providing referential information on the type of threat, alarm calls can also convey graded information on the degree of danger. Arabian babblers, *Turdoides squamiceps*, and great gerbils, *Rhombomys opimus*, use distinct vocalisations to communicate the proximity of the threat to the caller (Randall & Rogovin, 2002; Sommer et al., 2012), whereas white-browed scrubwrens and superb fairy-wrens, *Malurus cyaneus*, vary the number of elements in their aerial alarm calls according to how close the predator is (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). Black-capped chickadees also increase the number of elements in their mobbing alarm calls with greater danger, but their calls are adjusted on the basis of both predator size and proximity (Baker & Becker, 2002; Templeton et al., 2005). Meerkats produce distinct call types for aerial and terrestrial threats, but they show a consistent pattern for communicating urgency across contexts: noisier calls are given to closer threats (Manser, 2001). Individuals attend to this graded information in conspecific alarm calls by responding more intensely to alarm calls that indicate a more dangerous situation (Fallow & Magrath, 2010; Leavesley & Magrath, 2005; Manser et al., 2001; Randall & Rogovin, 2002; Templeton et al., 2005).

Alarm call structure

In addition to disentangling the meaning of alarm calls, the structure of alarm calls has been a subject of interest for understanding how function can affect signal design. In the 1950s, Peter Marler argued that flee alarm calls given to flying hawks should have acoustic properties to reduce detection and localizability, namely high frequency, low amplitude, narrow bandwidth, pure tones with a gradual onset and offset (Marler, 1955, 1957). Mobbing alarm calls, on the other hand, serve to recruit other individuals to the caller, selecting for features that increase detection and localizability (Marler, 1955, 1957). Consistent with this, many mobbing calls of European passerines are loud, low-pitched, broadband calls with an abrupt onset, while flee alarms show the opposite pattern in their

"seeet" structure (Marler, 1955, 1957). Several small mammalian species also give similarly high-pitched alarm calls to hunting raptors (Cäsar et al., 2012; Greene & Meagher, 1998; Le Roux et al., 2002; Melchior, 1971; Vencl, 1977). Furthermore, European raptors are less likely to detect and accurately locate these flee alarm calls than the mobbing calls, and European sparrowhawks are significantly less sensitive to higher frequency sounds around the 7-8 kHz range of flee alarm calls than the small birds upon which they prey (Klump et al., 1986).

Although the evidence from European passerines is suggestive of convergence in alarm call structure, not all species adhere to the described structural properties. The acoustic structure of flee, or aerial, alarm calls of Australian passerines varies considerably, even across related species (Fallow et al., 2011). The aerial alarm calls given by some Australian honeyeaters are relatively low in frequency (~4 kHz), have frequency sweeps and are loud (Jurisevic & Sanderson, 1994a; Wood et al., 2000); whereas members of the Maluridae and Acanthazidae families in Australia have high pitched calls (6 – 9 kHz), and some species' aerial calls show rapid frequency modulation, which should make them easier to locate (Brown et al., 1978; Cunningham & Magrath, 2017; Fallow et al., 2011). Orange-billed babblers, *Turdoides rufescens*, and greater racket-tailed drongos, *Dicrurus paradiseus*, in Sri Lankan rainforests also give frequency modulated aerial alarms that have low peak frequencies (2 – 4 kHz) (Goodale & Kotagama, 2008a). A study of the mobbing calls of 52 North American passerines found that there was a diversity in acoustic structure and only about half the species showed the features described by Marler, and a comparison of the mobbing calls of some North American and European species found evidence for both similarity and considerable variation in acoustic structure across species (Dutour et al., 2017; Ficken & Popp, 1996). Thus, there is clearly a diversity of alarm call structure both within and across regions. However, despite deviations from Marler's proposal, Australian and North American raptors nonetheless have been shown to find it easier to detect and locate broadband, or mobbing, alarm calls than the narrow band, aerial calls of the native species (Brown, 1982; Jones & Hill, 2001; Jurisevic & Sanderson, 1998; Wood et al., 2000).

Covert signaling to minimise the ability of predators to eavesdrop on alarm calls is not the only possible explanation for the structure of animal alarm calls. In many species of birds and mammals, sounds associated with aggressive contexts are generally low-pitched and harsh, whereas fearful or appeasement sounds tend to be high and pure (Morton, 1977). As such, the contrasting structures of flee and mobbing alarm calls, which prompt escape and approach respectively, could simply reflect constraints imposed by motivation-structural rules (Morton, 2017). Consistent with these structural rules, several species give higher pitched calls when the threat is closer to them, possibly reflecting increased fear (Fallow & Magrath, 2010; Ficken & Witkin, 1977; Leavesley & Magrath, 2005; Leger et al., 1979b). Additionally, animals could enhance detection of their alarm calls through sensory exploitation, by incorporating acoustic features that are difficult to ignore (Morton, 2017; Owren & Rendall, 2001). In several mammalian species, alarm calls associated with greater urgency or arousal are noisier than less urgent calls, a feature which has been shown to prompt stronger responses and renders the call more difficult to habituate to (Blumstein & Récapet, 2009; Coss et al., 2007; Fitch et al., 2002; Furrer & Manser, 2009; Karp et al., 2014; Manser, 2001; Townsend & Manser, 2011).

Alarm call reliability

False alarm calls are prevalent among birds and mammals, with many species producing over 20% of their alarms in the absence of predators and some species giving over 70% of their alarm calls to non-predators (Flower, 2011; Goodale & Kotagama, 2005a; Hollén et al., 2008a; Magrath et al., 2009a; Sommer, 2011). In most cases, this is likely to be due to the calling individual making mistakes or adopting a strategy of better safe-than-sorry (Haftorn, 2000; Magrath et al., 2009a). Juveniles, in particular, are prone to making classification errors (Hollén et al., 2008b; Radford & Hollén, 2009; Robinson, 1981). In some species, though, individuals produce false alarms to secure access to a desired resource or to defend their nest (Flower, 2011; Igic et al., 2015; Møller, 1988, 1990). Species in which individuals can either recognise the identity of the calling individual or the class of the caller can mitigate the costs of false alarms by showing reduced responsiveness to unreliable callers, or classes of caller (Blumstein et al., 2004a; Blumstein & Daniel, 2004; Gouzoules et al., 1996;

Ramakrishnan & Coss, 2000a; Seyfarth & Cheney, 1990; Sloan & Hare, 2006). However, even in species with high rates of false alarms, conspecific receivers still attend to the alarm calls, presumably as the price of ignoring true alarm calls could be death (Haftorn, 2000).

Heterospecific cues

In addition to using information from conspecifics, animals can also attend to the anti-predator behaviour of other species (heterospecifics). Indirect evidence for eavesdropping on heterospecific anti-predator cues comes from reduced investment in vigilance in the presence of other species (Jacobsen & Ugelvik., 1994; Kristiansen et al., 2000; Larsen, 1996). For example, zebras spend less time vigilant when foraging in mixed-species groups with giraffes, *Giraffa camelopardalis*, which have a superior view of the landscape, than when feeding with other zebras (Schmitt et al., 2016). Similarly, Thomson's gazelle, *Gazella thomsoni*, benefit from associating with Grant's gazelle, *G. granti*, because the taller Grant's gazelle are able to detect predators sooner (FitzGibbon, 1990). Tungara frogs, *Physalaemus pustoulosus*, appear to use heterospecific advertising calls as an all-clear cue following a predation event (Phelps et al., 2007). Several aquatic species respond to the chemical cues from damaged heterospecifics (Ferrari et al., 2010), showing evidence for phylogenetically conserved cues, as well as sensitivity to the size or shared vulnerability of the injured species (Anderson & Mathis, 2016; Dalesman et al., 2007; Elvidge & Brown, 2015). Observing heterospecific carcasses can also provide an indirect cue of predation risk, and western scrub-jays, *Aphelocoma californica*, increase their antipredator behaviour when exposed to dead heterospecifics, but only if they have a similar body size (Iglesias et al., 2014).

Heterospecific alarm calls

Eavesdropping on the alarm calls of other species is a widespread phenomenon. There is evidence of heterospecific eavesdropping both within and between birds and mammals, and even examples of reptiles attending to the alarm calls of birds (e.g. Ito et al., 2017; Müller & Manser, 2008; Rainey et al., 2004; Shriner, 1998; for review, see Magrath et al., 2015). Given the diversity of eavesdropping species, it is clear that species do not need to be social nor do they need to produce

their own alarm calls, or vocalisations at all, in order to eavesdrop on the alarm calls of other species (Fuong et al., 2014; Lea et al., 2008; Seiler et al., 2013). Eavesdropping may therefore play an important role in the transfer of information about danger within communities (Goodale et al., 2010).

Information available through heterospecific alarm calls

As alarm calls vary in the sorts of information they convey, eavesdropping individuals have a wealth of potential information available to them. There is evidence from both birds and mammals that some species are able to respond appropriately to the information provided by the functionally referential alarm calls of heterospecifics (Cheney & Seyfarth, 1985; Dawson Pell et al., 2018; Rainey et al., 2004a, 2004b). For example, vervet monkeys respond to the raptor alarm calls of superb starlings, *Spreo superbus*, by looking up or fleeing to cover (Cheney & Seyfarth, 1985). Individuals can also assess the urgency of heterospecific alarm calls: white-browed scrubwrens and superb fairy-wrens both include more elements in alarm calls given to closer threats, and both species are more likely to flee to conspecific and heterospecific alarm calls comprised of more elements (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). Although red-breasted nuthatches, *Sitta canadensis*, do not encode urgency in their own alarm calls, they approached speakers more closely when presented with black-capped chickadee mobbing calls associated with a smaller and more dangerous predator (Templeton & Greene, 2007).

While some species extract detailed information from heterospecific alarm calls, others show more generalised anti-predator responses. Although crowned plover, *Vanellus coronatus*, encode predator proximity in their alarm calls, banded mongooses, *Mungos mungo*, did not show stronger responses to more urgent plover calls (Müller & Manser, 2008). Several species respond to heterospecific alarm calls by becoming vigilant, a generalised response that should increase their personal information about the danger. An increase in vigilance is shown by pied babblers, *Turdoides bicolor*, to scimitarbill, *Rhinopomastus cyanomelas*, aerial alarms (Ridley et al., 2014), Malabar trogons, *Harpectes fasciatus*, to a range of heterospecific alarm calls (Goodale & Kotagama, 2008a), Zenaida doves, *Zenaida aurita*, to carib grackle, *Quiscalus lugubris*, ground alarms (Griffin et al., 2005),

Madagascan spiny-tailed iguanas, *Oplurus cuvieri cuvieri*, to Madagascar paradise flycatcher, *Terpsiphone mutata*, mobbing calls (Ito & Mori, 2009), white-bellied copper-striped skinks, *Emoia cyanura*, to red-vented bulbul, *Pycnonotus cafer*, harrier alarm calls (Fuong et al., 2014), and collared pikas, *Ochotona collaris*, to marmot and ground squirrel terrestrial alarm calls (Trefry & Hik, 2009).

Mechanisms of Heterospecific alarm recognition

Recently, there has been a growing interest in establishing how animals are able to recognise heterospecific alarm calls. The mechanisms could affect which species can eavesdrop on each other and determine how flexible community information networks are to changes in structure (Magrath et al., 2015a). As response to conspecific alarm calls can be innate (Davies et al., 2004; Radford & Hollén, 2009), some species are able to recognise unfamiliar alarm calls that have a similar acoustic structure to their own calls (Dutour et al., 2017; Fallow et al., 2011, 2013; Johnson et al., 2003). For example, superb fairy-wrens showed strong fleeing responses to allopatric and synthetic alarm calls with a similar peak frequency to their own aerial alarm calls (Fallow et al., 2011, 2013). Humans, *Homo sapiens*, are able to accurately assess emotional arousal in the calls of species from all classes of terrestrial vertebrates by attending to changes in frequency parameters (Filippi et al., 2017). Conserved signaling mechanisms across species can also facilitate responses. Great tits approached speakers more closely when played more urgent mobbing calls from the related but allopatric black-capped chickadees (Randler, 2012), and 15 songbird species across 5 communities increased their calling rate when giving a variable-use call in a predator context and responded more strongly to heterospecific calls presented at a faster rate (Wheatcroft, 2015).

While acoustic similarity may be sufficient to explain some examples of heterospecific eavesdropping, alarm calls can show considerable variation in structure (Magrath et al., 2015a). In these cases, there is evidence that familiarity with heterospecific alarms is required for response (e.g. Magrath et al., 2009b; Ramakrishnan & Coss, 2000; Wheatcroft & Price, 2013). Both wild birds and mammals can rapidly learn to associate unfamiliar natural and artificial sounds with danger, which makes learning a plausible mechanism for heterospecific call recognition, and there is some suggestive

evidence from natural examples of call recognition that learning may indeed take place (Magrath et al., 2015b; Shriner, 1999). For instance, superb fairy-wrens only respond to the alarm calls of noisy miners, *Manorina melanocephala*, at sites where both species occur, despite the fact that sites with and without miners are within fairy-wren dispersal distance (Magrath & Bennett, 2012). Furthermore, fledgling white-browed scrubwrens respond to conspecific alarm calls upon leaving the nest but do not acquire a response to heterospecific alarm calls until a few weeks after leaving the nest, with the time to acquisition reflecting heterospecific presence on their natal territory (Haff & Magrath, 2013).

Benefits of heterospecific eavesdropping

Eavesdropping on the alarm calls of other species may be particularly beneficial for some, as certain species may be better at detecting threats than others (Goodale et al., 2010). Social species with sentinel systems in which individuals take turns looking out for danger potentially provide more information on danger than species without sentinels, which may explain why solitary scimitarbills rely more heavily on the alarm calls of the social pied babbler than vice versa (Ridley et al., 2014). Species that feed upon insects often occupy perches high in the canopy and may therefore be in a better position to detect danger than substrate-feeding species (Goodale & Kotagama, 2008a; Martínez & Zenil, 2012). In support of this, studies on two different bird assemblages found that insectivorous species were less reliant on alarm calls than birds that fed closer to the substrate (Goodale & Kotagama, 2008a; Martínez & Zenil, 2012). Some species may lack alarm calls entirely or vocalise rarely, such as lizards or mule deer, *Odocoileus hemoinus*, making heterospecific calls a valuable source of information about predators (Carrasco & Blumstein, 2012; Ito et al., 2017; Ito & Mori, 2009; Vitousek et al., 2007). Even amongst species that do have alarm calls, some species have a greater propensity to call than others, affecting the availability of conspecific information and potentially increasing the reliance on heterospecific sources (Goodale & Kotagama, 2005a; Martínez et al., 2017).

Heterospecific alarm call relevance

Different species can be vulnerable to different suites of predators, leading to issues of alarm relevance for heterospecific eavesdropping (Magrath et al., 2015a). An alarm call will only be relevant to an eavesdropper if it is associated with the specific predators that pose a threat to it (Magrath et al., 2009a). It is therefore likely that many heterospecific alarm calls will only be partly relevant to eavesdroppers, which may share some but not all predators with the calling species (Magrath et al., 2015a). Eavesdroppers can deal with partial relevance by reducing their responsiveness to calls from species with which they share fewer threats or, if possible, by only attending to the subset of alarms that signal shared predators (Magrath et al., 2015a). Herring gulls, *Larus argentatus*, are smaller than great black-backed gulls, *L. marinus*, and show strong anti-predator responses to both species' alarm calls. The larger great black-backed gulls give a less intense response to herring gull alarm calls than to conspecific calls, suggesting that they grade their responses to the alarms according to the relevance (MacLean & Bonter, 2013). Similarly, red-vented bulbuls, which spend most of their time in trees and are therefore primarily vulnerable to aerial threats, do not respond to the alarm calls of common mynas, *Acridothere tristis*, that call to both aerial and terrestrial threats (Munoz et al., 2015). Instead of adjusting the magnitude of response, yellow- and black-casqued hornbills, *Ceratogymna elata* and C. *atrata*, which are preyed upon by eagles but not leopards, consequently only attend to the eagle alarm calls of sympatric monkeys (Rainey et al., 2004a, 2004b).

Furthermore, sensory constraints could limit reliance on heterospecific alarm calls: the responses of white-browed scrubwrens and superb fairy-wrens to heterospecific alarm calls were more strongly affected by attenuation and degradation than their responses to their own alarm calls, suggesting that the constraints on both detection and recognition are greater for heterospecific calls (Murray & Magrath, 2015). Dwarf mongooses, *Helogale parvula*, fled less frequently to heterospecific alarm calls when exposed to road-noise, but this could also be due to increased vigilance during high levels of background noise (Morris-Drake et al., 2017).

1.3 INTEGRATION OF INFORMATION

Animals thus have a rich diversity of information about threats available to them, either through detecting danger directly or by using the cues and signals of other individuals and species that can warn them about potential predators. However, relatively little work has been done to determine the relative value individuals place on the potential sources of information or how they integrate information from multiple sources. There is some evidence that individuals value personal and social information differently. In some cases, individuals with less personal information about the current danger can overestimate the degree of risk compared to individuals with more information (Frechette et al., 2014; Schneider & Griesser, 2013; van der Veen, 2002). Alternatively, individuals relying on social information may show more variable responses than individuals that can see the threat, reflecting their greater uncertainty (Lind et al., 2005; Wong et al., 2005). Animals may also differentially value information from different sensory modalities, such as stellar jays, *Cyanocitta stelleri annectens*, taking longer to resume feeding if they saw a model predator rather than heard predator calls (Billings et al., 2017), or two species of tadpoles showing the strongest avoidance behaviour in response to chemical rather than visual cues of a predator (Stauffer & Semlitsch, 1993). But having access to multiple sensory modalities and sources of information can ensure a level of redundancy, and consequently resilience, in predator detection (Hartman & Abrahams, 2000; Partan, 2017).

Animals can integrate multiple sources of information in different ways according to their value. These interactions can result in stimulus dominance, antagonism or enhancement (Munoz & Blumstein, 2012). Dominance occurs when individuals respond most strongly to one stimulus type, such as roach, *Rutilus rutilus*, reducing their time spent in open-water habitat when presented with visual and chemical predator cues, which is the same behaviour they show to visual cues alone and the opposite of what they do when presented with chemical cues (Martin et al., 2010). An antagonistic interaction results in individuals showing a diminished response when exposed to multiple cues, as is demonstrated by dark-eyed juncos, *Junco hyemalis*, showing a greater delay to respond when

presented with multiple alarm cues, an effect which is amplified when the alarm calls are coupled with a flushing bird (Randolet et al., 2014). Finally, individuals may show the greatest response when presented with multiple sources of information, resulting in stimulus enhancement. Several aquatic species respond most strongly when provided with both chemical and visual cues of predator presence (Lehtiniemi, 2005; McCormick & Manassa, 2008; Tikkanen et al., 1994), and reed warblers, *Acrocephalus scirpaceus*, are more likely to reject an experimental egg from their nests when they are presented with both a cuckoo, *Cuculus canorus*, model at their nest and conspecific alarm calls (Thorogood & Davies, 2016). Despite this handful of examples, our understanding of how animals integrate information about danger from multiple sources is limited. How individuals use the information available to them, and whether different sources provide complementary or redundant information on predators, may shape the information networks of communities and affect their resilience to change (Magrath et al., 2015a).

1.4 STUDY SPECIES AND SITE

In this thesis, I use a colour-banded population of New Holland honeyeaters, *Phylidonyris novaehollandiae*, in the Australian National Botanic Gardens, Canberra (35°16'S, 149°6'E) as a model system for investigating information production and use in the context of danger. These honeyeaters are an ideal species for addressing such questions. Firstly, they produce distinctive vocalisations in the presence of predators that can be easily recorded (see section 4.2 for more details on their calls). Secondly, previous work has found that these honeyeaters show a clear and easily quantifiable response to alarm calls of both their own and other species (Magrath et al., 2009a). Furthermore, their alarm calls are widely attended to by other species, and they may consequently play a particularly important role in the information networks of local communities.

The Australian National Botanic Gardens (ANBG) consist of a 40 ha area that features both natural vegetation and areas with planted Australian native fauna (Magrath, 2001). Over 100 species of bird have been recorded in ANBG (eBird, 2018). ANBG is open to the public and receives over

400,000 visitors per year (Connery, 2017). Consequently, birds within the gardens are habituated to people and tolerate approach to within a few metres (personal observation). The gardens are home to a resident population of around 70 New Holland honeyeaters. Detailed work on the alarm calling behaviour of several resident bird species by Robert Magrath and his students makes it an excellent site for studying communication about danger in avian communities (e.g. Fallow & Magrath, 2010; Igic & Magrath, 2014; Magrath et al., 2009a).

General biology

The New Holland honeyeater is a small (20 g) songbird found in south-eastern and south-western Australia (Higgins et al., 2001). They forage singly, in pairs or in small groups, but they can also gather in large numbers at rich food sources (Higgins et al., 2001; McFarland, 1986b). Honeyeaters primarily feed upon nectar, which is obtained by probing flowers (Paton, 1980). They also glean and sally for insects, as well as feeding upon manna, a sugary exudate from damaged plants, and lerp, a carbohydrate-based protective covering of Australian psyllids (Paton, 1980, 1982). They are mainly arboreal, feeding in the canopy and shrub layer but rarely on the ground (Higgins et al., 2001). Pairs, or single males, defend territories of 375 – 530 m^2 in size from which conspecific and other nectar-feeding intruders are excluded (Higgins et al., 2001; McFarland, 1996). Territories are based around the preferred perches of males, rather than the nest site (Armstrong, 1991). The use of perches does not appear to function as territory or sexual advertisement by the males, as it does not vary according to season or breeding cycle (Armstrong, 1996). As birds frequently feed outside their territories as well, there is a dominance hierarchy amongst neighbours in which the most dominant bird at a feeding site is the bird with the closest territory (McFarland, 1994; Rooke, 1979).

New Holland honeyeaters form socially monogamous breeding pairs (Higgins et al., 2001). While the honeyeaters can breed all year round, they generally breed for about 8 months of the year with peaks in spring and autumn (Armstrong & Pyke, 1991; McFarland, 1986a; Paton, 1985; Recher, 1977). The sexes are monochromatic (Fig. 1.1, p 25), but males are larger than females on average (Ford & Paton, 1982; Myers et al., 2012; Pyke & Armstrong, 1993; Rooke, 1979). Only females build

the nest, incubate and brood the young, whereas males carry out most of the territory defense (Paton, 1985; Recher, 1977; Rooke, 1979). Males perch near the nest during nest building and incubation, and remain near the female when she leaves the nest to feed (Higgins et al., 2001; Rooke, 1979; personal observation). Both sexes feed their offspring until independence, around 4 weeks after fledging (Higgins et al., 2001). Male offspring sometimes settle close to their natal territory (Armstrong, 1990; Higgins et al., 2001). There is a male-biased sex ratio amongst adult honeyeaters, due to higher rates of mortality in females (Higgins et al., 2001).

Figure 1.1. *Photographs of female (above) and male (below) New Holland honeyeaters (not to scale). Sexes are monochromatic, but males are slightly larger. Photographs by Jessica McLachlan.*

Vocal behaviour

The vocal repertoire of the New Holland honeyeater has not been studied in great detail, but birds produce a range of single note and multi-note calls in social contexts, as well as multi-note calls given during chases and corroboree gatherings (Fig. 1.2, p 27) (Jurisevic & Sanderson, 1994b; Rooke, 1979). Corroborees generally comprise largely of males that call noisily in a group while adopting wing-fluttering postures (Pyke & O'Connor, 1993; Rooke, 1979). Only males produce a song, a soft vocalisation given during song flights (Fig. 1.2d). It is one of the quietest sounds in their repertoire. They sing most often in the week before laying, and the song appears to encourage the female to go to the nest (Rooke, 1979). Both sexes vocalise during copulations (Fig. 1.2e) (personal observation).

Alarm calls are the best studied vocalisations of the New Holland honeyeater, particularly in relation to raptor perception (Jurisevic & Sanderson, 1994a, 1998; Rooke & Knight, 1977; Wood et al., 2000). They are distinct from the honeyeaters' other vocalisations (Fig. 1.3, p 28). In addition to giving distress calls (Fig. 1.3a) when in the hand or when attacked by conspecifics, honeyeaters produce two distinct alarm calls: a chatter call (Fig 1.3b) and a whistle call (Fig. 1.3c) (Jurisevic & Sanderson, 1994a; Rooke, 1979; Rooke & Knight, 1977; Wood et al., 2000; personal observation). The chatter call is given to slow-moving, ground predators, such as foxes and snakes. It consists of repeated, short, broadband notes with frequency modulations and a peak frequency of 5.7 kHz (Jurisevic & Sanderson, 1994a). Notes increase in amplitude and duration with increasing alarm (Jurisevic & Sanderson, 1994a). It is audible up to around 30 m away (Rooke, 1979). The whistle call is used in association with flying predators or when startled by ground predators (Jurisevic & Sanderson, 1994a; Rooke, 1979; Rooke & Knight, 1977). It is much louder than the chatter alarm call, and can be heard 500 m away (Rooke, 1979). It is also composed of repeated, short notes but they are tonal with descending frequency sweeps and a peak frequency of 4 – 4.5 kHz (Jurisevic & Sanderson, 1994a; Magrath et al., 2009a).

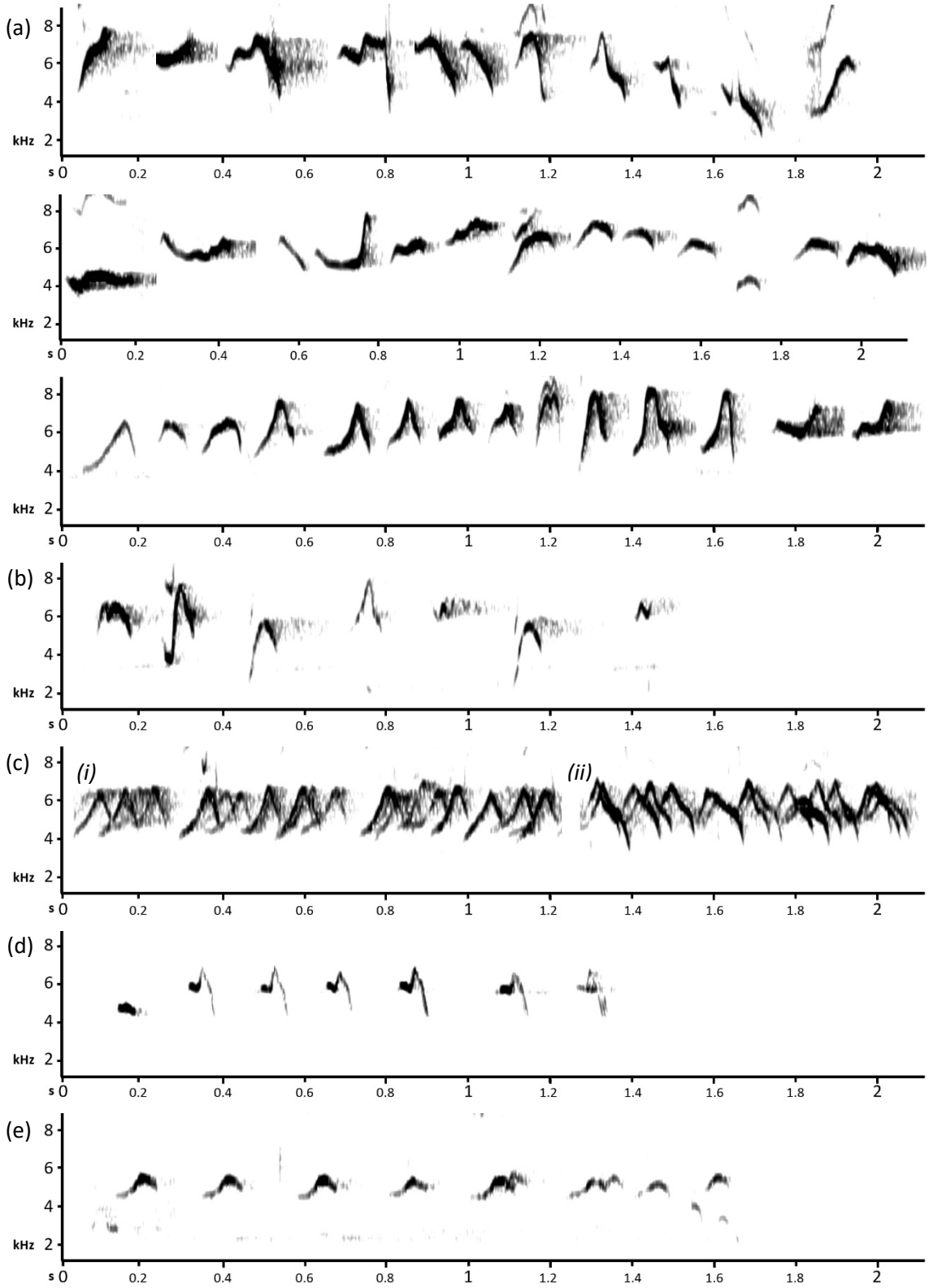


Figure 1.2. *Spectrograms of calls used in social contexts. Examples of a) notes of unknown functions recorded from male and female honeyeaters calling during social interactions or from perches, b) sequence of calls given during a chase, c) calls given by multiple individuals during two corroborees (i & ii), d) flight song, and e) copulation calls. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz.*

Playbacks of whistle alarms prompt immediate flight to cover in conspecifics, providing an unambiguous response measure (Magrath et al., 2009a), and a wide range of heterospecifics appear to attend to this call, ranging from other small birds, like white-browed scrubwrens and western spinebills, *Acanthorhynchus superciliosus*, to predatory species, like the pied currawong, *Strepera graculina*, and Australian ravens, *Corvus coronoides* (Igic et al., 2015; Magrath et al., 2009a; Rooke & Knight, 1977; personal observation). These attributes make the whistle alarm an excellent system for investigating the rapid transfer of information between individuals, and I consequently focused on this alarm call for my thesis.

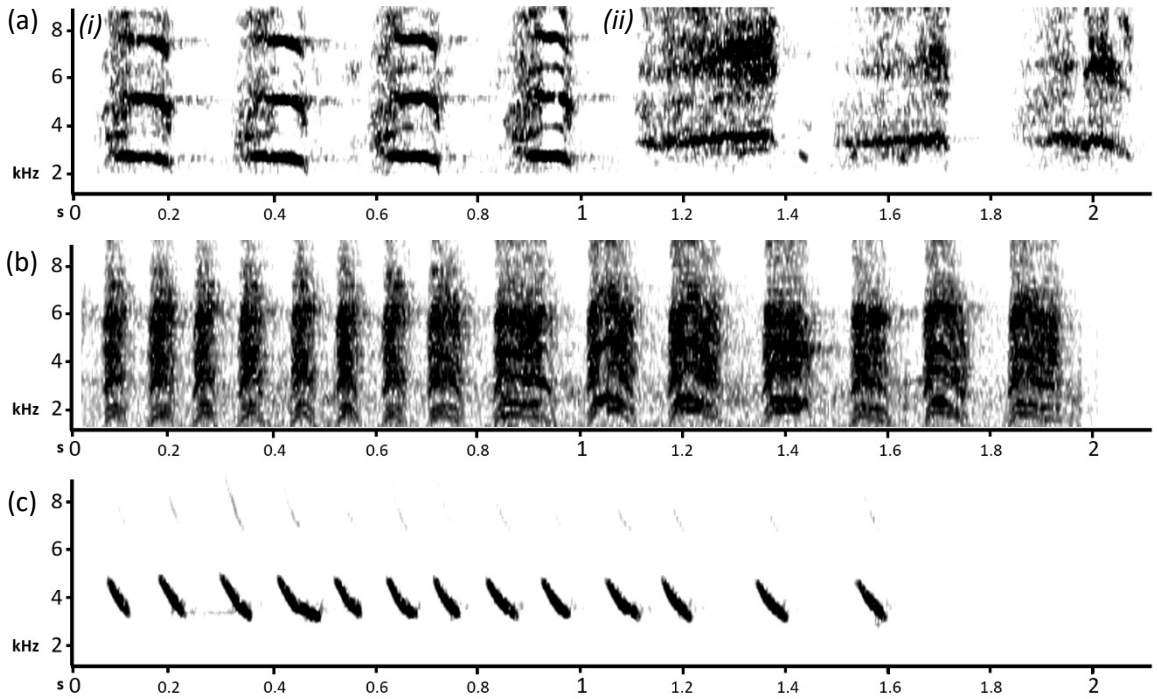


Figure 1.3. *Spectrograms of alarm vocalisations. a) Distress calls recorded from two individuals (i & ii) caught in mist nets, b) chatter (mobbing) alarm call given to a snake, and c) whistle (aerial) alarm call given to a flying threat. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz.*

1.5 THESIS OVERVIEW AND AIMS

In this thesis, I investigate: 1) how individuals communicate about danger, and 2) how receivers can integrate the information available to them from multiple sources. To address these questions, I use a combination of natural observations, playback experiments and presentations of model predators. The relatively recent development of lightweight consumer video cameras and rigs made it possible to construct a mobile video and sound recording system that allowed me to film the responses of birds, resulting in detailed data on the timing of their behaviours as well as an opportunity for blind-scoring of the data (Fig. 1.4, p 30).

This thesis consists of six chapters, including this introductory chapter and a short summary chapter. The remaining four data chapters are written in the form of stand-alone research articles as a prelude to separate publication, and there is consequently some repetition in the introduction and method sections of some chapters. Chapters 2 and 3 address the production of information about danger, while Chapters 4 and 5 are concerned with how receivers use this information.

In Chapter 2, I use natural observations to confirm the context in which New Holland honeyeaters give whistle alarm calls and to establish which individuals produce the calls. I determine whether the sex-biased production of the alarm calls arises from differences in the likelihood of detecting threats or in the propensity to give a call in the presence of a predator.

Chapter 3 addresses how honeyeaters encode information in their alarm calls. I begin by examining how the degree of danger affects both number of elements given in a call and the acoustic structure of those alarm elements during natural predator encounters and model presentations. I then investigate what information receivers extract from conspecific alarm calls using a series of playback experiments.

Having established the production context and information content of honeyeater alarm calls in the above two chapters, I proceed to explore how individuals use the information from alarm calls in conjunction with other possible sources and how the quantity and quality of that information affects their behaviour.

In Chapter 4, I ask whether honeyeaters value their personal information about danger above the social information provided by alarm calls. I take advantage of natural variation in the behaviour of honeyeaters to ascertain whether birds probing flowers for nectar have reduced personal information compared to birds perched on exposed branches. I use a series of playback experiments to test if foraging birds respond more strongly to alarm calls than perched birds, and to see whether the quality of the social information affects its value.

Chapter 5 examines how birds use social information from multiple sources. I first look at how honeyeaters adjust their responses based on the number of conspecific alarm calls and the number of conspecific callers. I follow this by investigating the effect of the number of calling species on their behaviour, by presenting playbacks of alarm calls from either two different heterospecific species or from a single heterospecific species, where the relative reliability of the species presented varied across experiments.

Figure 1.4. *Photographs showing the playback, sound and video recording equipment used for experiments. Photographs taken by Nicholas Borner.*

Chapter 2

Sex-biased production of an aerial alarm call

2.1 SUMMARY

Despite the high stakes associated with predator encounters, few studies consider which individuals, or classes of individuals, give alarm calls. Here I confirm the context in which New Holland honeyeaters produce “whistle” alarm calls and establish which individuals are responsible for their production by carrying out natural observations and presenting birds with gliding model predators. The honeyeaters gave whistle alarms primarily in response to flying predators, which is consistent with previous work that suggested they are used as aerial alarm calls. But the production of the alarm calls was strongly sex-biased: male honeyeaters were more likely to produce whistle alarms than females during focal observations on individual honeyeaters. This difference in call production could be driven by either a difference in the likelihood of detecting threats or in the probability of calling when a threat has been detected. I found that male honeyeaters spent considerably more time perched than females, providing them with more opportunities to spot flying predators. However, when perched birds were presented with a flying model predator, males honeyeaters were more likely to give an alarm call than females, even though both sexes were equally likely to flee in response. This suggests that there are fundamental differences in the alarm calling behaviour of male and female New Holland honeyeaters.

2.2 INTRODUCTION

Many animals produce alarm calls that signal the presence of predators (Caro, 2005). These signals can be general indicators of danger or they can warn of specific types of threats, most commonly to indicate the presence of either flying or ground predators (Gill & Bierema, 2013; Suzuki, 2016). Using distinct alarm calls to signal about different classes of threat allows receivers to better detect threats (Suzuki 2018), and to adopt appropriate threat-specific responses. Alarm calls prompted by ground predators are often low, broadband calls that recruit conspecifics to mob the threat (Marler, 1955, cf. Ficken & Popp, 1996), whereas aerial alarm calls are given to predators in flight and are commonly high-pitched, narrow-band vocalisations that elicit a fleeing or freezing response from listeners (Marler, 1955; Searcy & Yasukawa, 2017). Despite the large body of literature on alarm calls, detailed observational studies of the natural context of alarm calling are not common, but they are nonetheless important for establishing which individuals call and in what contexts.

Alarm calling is often assumed to impose a cost on the caller as, by vocalising, it makes itself conspicuous to the threat. However, direct evidence of any such costs, or benefits, to the caller is sparse. The common acoustic structure of aerial alarm calls renders them hard to hear or locate (Bayly & Evans, 2003; Brown, 1982; Jones & Hill, 2001; Klump et al., 1986; Krams, 2001; Wood et al., 2000). This suggests that there may have been a cost in the past to calling in the face of danger, which has selected for vocalisations that are difficult to detect or locate, but aerial alarm calls may now be cheap to produce as a result of this adaptation. There could still be some cost to production: several species show clear audience effects, suppressing calling in the absence of mates or kin (Griesser & Ekman, 2004; Gyger et al., 1988; Sullivan, 1985), and individuals appear to preferentially call from positions of relative safety (Alatalo & Helle, 1990; Devereux et al., 2008). Two studies, however, have found that individuals that produced aerial alarm calls were less likely to be attacked, suggesting calling may in fact be beneficial to the caller (Kareksela et al., 2013; Sherman, 1985). Mobbing calls, on the other hand, tend to be easy to locate due to their broad-frequency range (Marler, 1955), which facilitates recruitment to the caller. These calls seem to be effective in persuading predators to hunt elsewhere,

benefiting the local prey community (Pavey & Smyth, 1998; Pettifor, 1990). But mobbing can come at a cost to the caller, by increasing the risk of nest predation (Krama & Krams, 2005) or even resulting in the death of the mobbing individual itself (Poiani & Yorke, 1989).

Given the potential costs and benefits of being the individual to call when a threat is nearby, it is surprising that there are relatively few studies that look in detail at the identity of the alarm callers. In social species, individuals may take on the role of watching out for, and informing their flockmates of, approaching danger (McGowan & Woolfenden, 1989; Ridley & Raihani, 2007; Sommer, 2011). While individuals take turns at performing this sentinel duty, their propensity to do so can be affected by their body condition (Bednekoff & Woolfenden, 2003; Wright et al., 2001a), dominance status (Wright et al., 2001b) and sex (Walker et al., 2016; Yasukawa & Cockburn, 2009). Individuals have also been found to vary in the likelihood of producing alarm calls in species that lack a sentinel system. Male jungle fowl, *Gallus gallus*, are responsible for the majority of aerial alarm calls (Palleroni et al., 2005), and their production has been linked to testosterone, a male sex hormone (Gyger et al., 1988). In black-capped chickadees, *Poecile atricapillus*, and song sparrows, *Melospiza melodia*, birds with bolder personalities give more mobbing calls (Guillette & Sturdy, 2011; Hyman et al., 2013).

The alarm calls of many birds, including some Australian honeyeaters, do not fully conform to the structural features set out by Marler (1955), and it has been suggested that the acoustic structure of the honeyeaters' aerial alarm calls should in fact make them easy to detect (Jurisevic & Sanderson, 1994b; Rooke & Knight, 1977; Searcy & Yasukawa, 2017; Wood et al., 2000). New Holland honeyeaters are reported to give a descending whistle call of relatively low frequency that is prompted by flying predators, as well as a broadband call given to ground predators (Jurisevic & Sanderson, 1994b; Rooke & Knight, 1977). I focused on their "whistle" alarm call because it is unusually loud for an aerial alarm, audible up to 500m away (Higgins et al., 2001), and the callers are often perched in exposed positions and easy to locate. This makes it a tractable system in which to study the identity of the alarm calling individuals.

Here I used both detailed observations and a model presentation experiment to confirm the context in which New Holland honeyeaters give alarm calls, and to determine which individuals produce the calls. First, I carried out observation sessions to record the types of prompts to which the honeyeaters produce "whistle" alarm calls with the expectation that these calls would be given to flying threats. Next, I conducted focal observation sessions on male and female honeyeaters to look for sex differences in alarm call production, as differences in alarm calling, a conspicuous behaviour for New Holland honeyeaters, could have important implications for survival. Finally, I used both observations and presentations of model flying predators to investigate possible behavioural mechanisms for sex-biased call production.

2.3 METHODS

Study site and species

Data were collected on a colour-banded population of New Holland honeyeaters between November 2014 and September 2015 in the Australian National Botanic Gardens in Canberra, Australia. New Holland honeyeaters are small (20 g), pair-breeding passerines that feed primarily on nectar from flowering plants. The birds in the study population were all resident in the botanic gardens, a 40 ha area of both natural and planted vegetation, and were accustomed to the presence of people. There are around 70 individuals in the gardens, and about 75% of the population has been colour-banded.

New Holland honeyeaters are territorial in the sense that males defend an area close to their nest site and are more dominant in interactions closer to the nest or the centre of the territory, but individuals forage over a much larger area and gather in big groups (>20 individuals) in association with flowering plants (Armstrong, 1991, 1996; Major et al., 1994; Pyke & O'Connor, 1993; personal observation). They are capable of breeding all-year round, with peaks in autumn and spring (Armstrong & Pyke, 1991; McFarland, 1986a; Paton, 1985; Recher, 1977).

New Holland honeyeaters give two distinct alarm calls (Jurisevic & Sanderson, 1994b; Rooke & Knight, 1977): a noisy, broadband "chatter" call that is primarily used in response to terrestrial threats and a "whistle" call, which is given to aerial threats and is composed of multiple elements of similar structure (Fig. 2.1). A whistle call can contain between 1 and 100 elements (personal observation). Each element consists of a pure, descending whistle of approximately 33 ms (mean ± SE: 33.66 ms ± 0.05, n = 20054 elements from 31 individuals) in length. The elements are loud, with an amplitude of about 70 dB at 6 m, and relatively low in pitch (peak frequency mean ± SE: 3541.19 Hz ± 1.7, n = 20054 elements from 31 individuals).

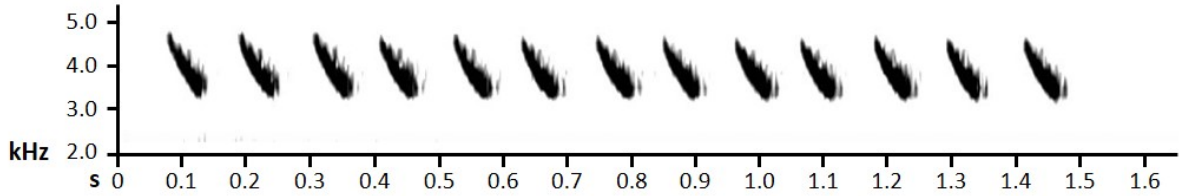


Figure 2.1. *An example of a New Holland honeyeater "whistle" alarm call. The spectrogram was produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz.*

Sexing

In order to determine sex differences in anti-predator behaviour, I needed to sex individuals within the population. To do this, I used three methods: 1) morphology, 2) behaviour, and 3) DNA analysis. Male honeyeaters are larger than females, making sexing based on morphology possible (Rooke, 1979). Previous work used a simple threshold rule for the head-bill measurement to discriminate between the sexes, but a more recent study suggests that the best traits for discrimination were not consistent across different populations (Myers et al., 2012; Pyke & Armstrong, 1993). Body size measurements were collected from adult New Holland honeyeaters caught in mist nets in the botanic gardens. The following five measurements were taken: (1) body mass, (2) wing length, (3) tail length, (4) head-bill length, and (5) tarsometatarsus length. All measurements were made by the same bander (RM). Head-bill and tarsometatarsus length were measured using calipers (accuracy = 0.01 mm). Body mass was measured using a Pesola balance (accuracy = 0.05 g). Wing and

tail length were measured using a stopped wing-rule (accuracy = 1 mm). In order to confirm the sex of banded individuals, a subset of birds were sexed by using blood samples (19 individuals); or observing sex-specific behaviours, such as nest building or incubating (only females), copulation position (females below) and song-flight displays (only males), during the breeding season (36 individuals); or both (7 individuals) (Higgins et al., 2001; Rooke, 1979). This resulted in a data set of 77 adult birds: 32 females and 23 males that were used to generate a linear discriminant function based on their body size measurements, and 22 individuals of unknown sex that were sexed morphologically using the linear discriminant analysis (see *Statistical analyses*). Blood samples were sent to DNA Solutions, Victoria, Australia for analysis, where the DNA was extracted from red blood cells using the Chelex technique, and the sex was determined by PCR amplification of the CHD1-W and CHD1-Z genes on the avian sex chromosome using P2 and P8 primers to reveal single (male) and double (female) bands (Griffiths et al., 1998).

Alarm Context Observations

To confirm whether whistle calls are primarily given to flying predators, as suggested by previous work (Magrath et al., 2009a; Rooke & Knight, 1977; Wood et al., 2000), I conducted 6 sets of 1 hour observations on alarm calling behaviour at each of 12 sites in the Australian National Botanic Gardens between November and December 2014. I observed 48 colour-banded individuals across the areas, as well as several unbanded birds within each area, so repeated data from a single individual is unlikely to have been a significant problem. The sites were based around popular feeding areas in the gardens, but some honeyeaters travelled between feeding sites and, where possible, the identities of the individuals present were also recorded (Fig. 2.2, p 40). Birds within the focal area were followed at a distance of 10 – 20 m, and any calls they gave were recorded using a Marantz PMD661 solid-state digital recorder with a sampling rate of 44.1 kHz at 16 bits, and a Sennheiser ME66 shotgun microphone. Where possible, I noted the probable prompt of any alarm calls given during the observation period and the identity of the calling individual. Previous work shows that the whistle call is an alarm call that is given to flying predators and gliding model predators, but it has also been

reported to be given in response to non-predators and non-flying species (Jurisevic & Sanderson, 1994a). As such, for each whistle bout, I recorded if there was a flying predator present. If I did not observe a flying predator, I recorded whether there was a non-flying predator present, a flying non-predator in close proximity to the calling bird, or a sudden appearance of a non-flying non-predator. Observations were conducted throughout the day, and each site received three observation sessions in the morning and three in the afternoon. Recordings were analysed in Raven Pro 1.4 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz.

Sex Differences Observations

As the results from the context observations were suggestive of a possible sex difference in alarm calling, I carried out 6 sets of 1 hour focal observations on the alarm calling behaviour of 20 colour-banded individual New Holland honeyeaters, 10 males and 10 females, between June and August 2015. Birds within the focal area were followed at a distance of 10 – 20 m, and any calls they gave were recorded using a Marantz PMD661 solid-state digital recorder with a sampling rate of 44.1 kHz at 16 bits, and a Sennheiser ME66 shotgun microphone. If I lost sight of the focal individual during the observation session, the clock was stopped and timing resumed only when I had relocated the bird. While the sample originally included paired birds, 5 pairs separated and changed partners over the observational period. Recordings were analysed in Raven Pro 1.4 (see above).

Figure 2.2. *Map of Australian National Botanic Gardens showing the areas where the observations were carried out and the identity of all banded individuals observed in each area during the observation sessions. Unbanded birds were also present in all areas. Stars beside birds indicate which individuals were known to have nest sites in the area.*

Time Budget Observations

Given the observed differences in calling, it was important to quantify the proportion of time individuals of each sex spent perched with a good view of their surroundings, which could result in a greater likelihood in predator detection. Therefore, in September 2015, I carried out 1 hour focal observations on 8 male and 8 female honeyeaters. Birds were followed at a distance of 10 – 20 m, and I recorded the amount of time (s) the individual spent perched during the observation period. I used two stop watches, one to ensure each focal session was 1 hour long and the other to record the perching time by starting the watch every time the focal bird landed on a perch and stopping it whenever the bird ceased perching. If I lost sight of the focal individual during the observation session, the clock recording the length of the session was stopped and timing resumed only when I had relocated the bird. Birds that spent more time perched were assumed to be more likely to see potential threats (Greig-Smith, 1981; Radford et al., 2009; Ragusa-Netto, 2002).

Model Presentations

It is difficult to disentangle from observational data alone whether differences in calling rate are due to differences in detection or differences in the probability of calling when a threat is detected. I therefore presented 14 male and 14 female New Holland honeyeaters with gliding model predators in August 2015. Each bird was presented with the model when they were perched with a clear view, approximately 10 – 15 m from the thrower, and their vocal response was recorded with a Marantz PMD661 Mk II solid-state digital recorder with a sampling rate of 44.1 kHz at 16 bits, and a Sennheiser ME 66 shotgun microphone. I also noted down the response of the bird, whether it fled to cover or scanned during the presentation, to confirm that the bird had indeed seen the model. Models were thrown such that they flew approximately parallel to the focal bird, rather than directly towards them. However, model trajectories varied unpredictably on every throw. If the bird appeared not to detect the model predator, the presentation was repeated later in the day. Two life-sized gliding model predators were used: they were made out of foam cut with hot wire and were painted to resemble

adult and juvenile collared sparrowhawks, *Accipiter cirrhocephalus* (Fig. 2.3). Recordings were analysed in Raven Pro 1.4 (see above).

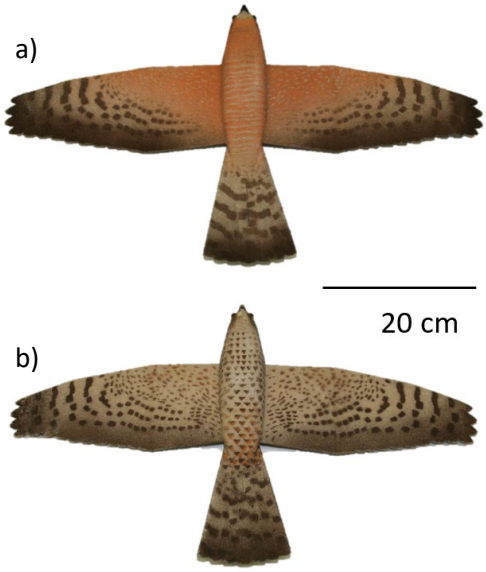


Figure 2.3. *Ventral view of gliding model predators resembling a) an adult and b) a juvenile collared sparrowhawk. Photographs by Rob Magrath. Models made by Alastair Smith.*

Statistical analyses

General statistical protocol

All statistical analyses were carried out in R version 3.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Binomial tests were carried out using the binom.test() function. T-tests, MANOVA and Pearson product-moment correlation tests were conducted using the t.test(), manova() and cor.test() functions, respectively. The linear discriminant function analysis was generated using the lda() function of the MASS package (Ripley et al., 2017). Generalised linear mixed effects models were constructed with binomial error distributions and logit link functions, using the glmer() function of the lme4 package (Bates et al., 2016). I constructed the linear mixed effects models with normal error distributions and identity link functions, using the lmer() function of the lme4 package (Bates et al., 2016). In all cases, the full model with all terms of interest was fitted before likelihood ratio tests were used to identify significant fixed effects.

Sexing

T-tests were carried out to test whether the morphological measurements could be used to distinguish between adult male and female honeyeaters. I used a multivariate analysis of variance (MANOVA) to test whether the sexes varied in body size across all measures. A linear discriminant function analysis was performed on the data from the 55 individuals of known sex, either through genetics or behaviour, to establish classification criteria that accurately discriminated the sexes on the basis of morphological measurements and could be applied to individuals of unknown sex. I tested for the association between the five morphological measurements using Pearson product-moment correlation tests. Because wing length was highly positively correlated with both tail length and head-bill measurements, wing length was discarded from the analysis. The priors were set to 0.5 for females and males, as the sex ratio of the local population was unknown. The model was validated using a jackknife cross-validation procedure.

Sex Differences Observations

In order to examine the effect of sex on the probability of alarm calling by individuals during the focal observation sessions, I constructed a generalised linear mixed effect model. Alarm calling was entered as the binomial response term, where 1 indicated that the bird had given at least one alarm call during the observational session and 0 meant that the bird had not called during the session. Bird sex and the amount of time I lost sight of each individual were entered into the model as fixed effects, and the identity of individual birds was included as a random effect to account for the repeated measures on individuals.

I used a linear mixed effect model to look at the effect of sex on the number of elements given during the observation sessions using a subset of the original data that only included sessions in which birds gave alarm calls. The number of elements was log-transformed to improve the fit before being entered as the response variable into a linear mixed effects model. Bird sex was entered into the model as a fixed effect and the identity of individual birds and the sessions were included as random effects.

Time Budget Observations

To determine the effect that bird sex has on the amount of time an individual spent perched, I used a linear model with the number of seconds a bird spent perched as the response variable. Bird sex and the amount of time I lost sight of each individual were entered as fixed effects. Perch time was log-transformed to improve the model fit.

Model Presentations

I constructed a general linear model to look at the effect of sex on the probability of a bird giving an alarm call when presented with a gliding model. The probability of alarm calling was entered as a binomial response variable, and the sex of the bird, the distance at which the predator model was presented in metres and the predator model type (adult vs juvenile) were entered as fixed effects.

2.4 RESULTS

Sexing

Males were larger on average than females (MANOVA: Pillai's $F_{5, 49} = 42.01$, $p < 0.001$; Table 2.1; Fig. 2.4, p 45). The discriminant function generated from individuals of known sex was:

D = -61.5 + -0.181(Weight) + 0.167(Tail) + 1.165(Head-Bill) + 0.161(Tarsus).

If D>0, birds were classified as male. Individuals that scored D<0 were classified as female. Following the jackknife validation procedure, the discriminant function equation classified 94.5% of the birds correctly (93.9% of females, 95.7% of males). This function could then be applied to sex adult birds of unknown sex.

Morphological measurements	Mean ± SE		LDA	T-test	
	Female	Male	Factor loading	*t*	p
Weight (g)	18.98 ±0.29	20.89 ±0.27	-0.18	-4.80	<0.0001
Wing length (mm)	73.69 ±0.31	78.65 ±0.49		-8.65	<0.0001
Tail length (mm)	73.84 ±0.47	79.87 ±0.82	0.17	-6.41	<0.0001
Head-bill length (mm)	40.48 ±0.14	43.18 ±0.17	1.16	-12.36	<0.0001
Tarsometarsus length (mm)	21.56 ±0.12	22.55 ±0.13	0.16	-5.78	<0.0001

Table 2.1. *Morphological characteristics of male and female New Holland honeyeaters, and outcomes of t-tests.*

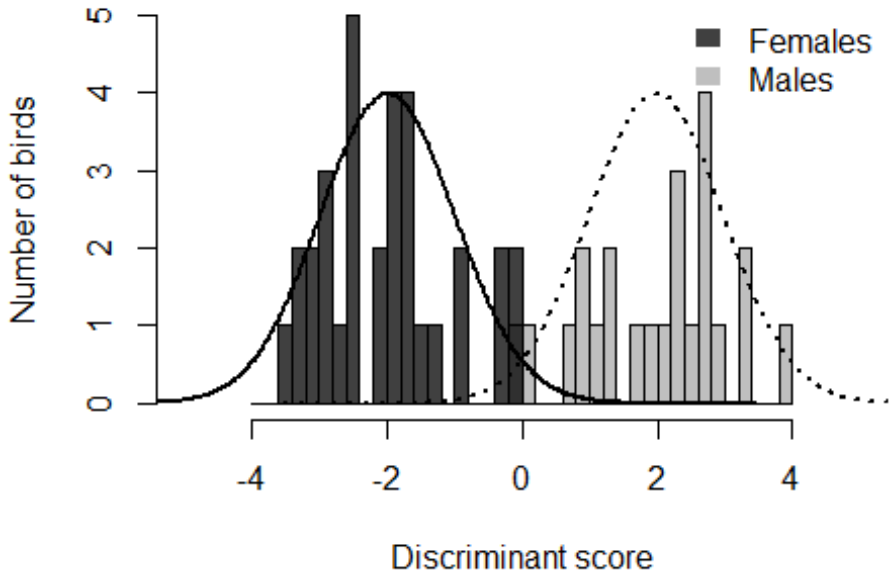


Figure 2.4. *The discriminant scores calculated for male and female New Holland honeyeaters. n=55.*

Alarm Context Observations

I recorded 254 whistle calling bouts during the 72 hours of observations. I was only able to identify the prompt for 57 of these bouts (Table 2.2), as the calling bird was often perched high in the canopy and calls lasted less than 1 s. Predators were present in 68% of the bouts with known prompts (Fig. 2.5, p 46). Of the bouts given to predators, 82% were prompted by predators in flight (Fig. 2.5). Both of these findings are consistent with the call being used as an aerial alarm call to signal the presence of a flying predator.

Non-predator Prompts	**Predator Prompts**
Australian magpie (*Gymnorhina tibicen*)	Australian raven (*Corvus coronoides*)
Crimson rosella (*Platycercus elegans*)	Collared sparrowhawk (*Accipiter cirrhocephalus*)
Gang-gang (*Callocephalon fimbriatum*)	Grey butcherbird (*Cracticus toquatus*)
Human (*Homo sapiens*)	Grey shrike-thrush (*Colluricincla harmonica*)
Red wattlebird (*Anthochaera carunculata*)	Laughing kookaburra (*Dacelo novaeguineae*)
Sulphur-crested cockatoo (*Cacatua galerita*)	Pied currawong (*Strepera graculina*)

Table 2.2. *List of species that prompted "whistle" alarm calls.*

I observed more males producing calls than females across the observations, as 86% of the identified callers were male. This is suggestive of a sex difference in calling behaviour, but the observational data could be due to other differences, such as males being more conspicuous or easier to follow, or the population having a skewed sex ratio.

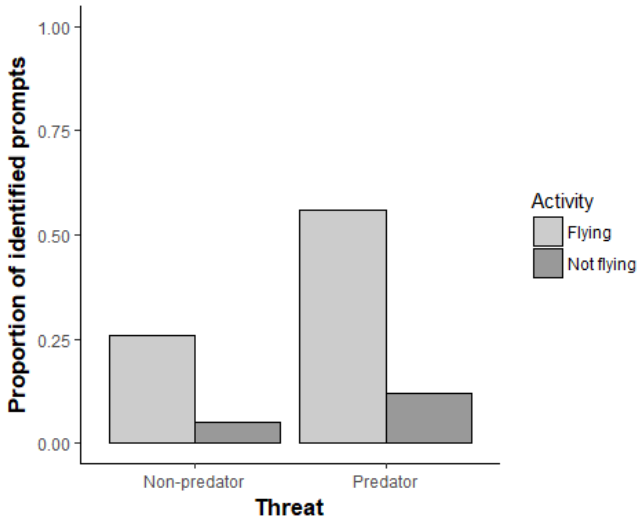


Figure 2.5. *Proportion of identified prompts according to the type of threat and the activity in which it was engaged. Light grey columns represent flying threats. Dark grey columns represent threats that were not in flight. N = 57 prompts.*

Sex Differences Observations

Male New Holland honeyeaters gave more alarm calls than females during the focal observations (Fig. 2.6, p 48). Male honeyeaters were more than twice as likely to give an alarm call than females (Table 2.3a, p 47; Fig. 2.6a). Furthermore, including only the sessions in which the focal individual gave at least one alarm call, male honeyeaters produced over six times as many alarm elements per session than females (Table 2.3b; Fig. 2.6b).

The difference between the sexes in their alarm call production could be due to differences in how likely the sexes are to see threats or because males are more likely to call when they detect a threat. In fact, males gave around 80% of their alarm calls when perched, whereas only 2% of female alarm calls were produced when perched (Table 2.3c; Fig. 2.6c). This difference in location, in combination with the higher calling rate in males, means it is important to compare both perch use in males and females, and their probability of calling when a predator is sighted.

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Observation sessions (GLMM)	**Probability of giving an alarm call**						
		(Intercept)		-1.12±0.66			
		Sex (Female)	Male	1.89±0.48	**1**	**14.19**	**0.00017**
		Lost Bird Time		-0.00±0.00	1	0.15	0.70
	Random term	*Bird - variance*		0.16			
		Session - variance		0.00			
(b) Observation sessions (LMM)	**Number of elements given**						
		(Intercept)		1.40±0.50			
		Sex (Female)	Male	2.30±0.59	**1**	**13.02**	**0.0003**
	Random term	*Bird - variance*		0.10			
		Session - variance		0.00			
(c) Observation sessions (GLMM)	**Probability of calling when perched**						
		(Intercept)		-4.66±2.15			
		Sex (Female)	Male	5.47±2.38	**1**	**5.15**	**0.02**
	Random term	*Bird - variance*		14.22			
		Session - variance		2.37			
(d) Perching behaviour (LM)	**Time spent perched**						
		(Intercept)		6.83±0.24			
		Sex (Female)	Male	0.97±0.19	**1**	**17.69**	**<0.0001**
		Lost Bird Time		-0.00±0.00	1	0.42	0.52
(e) Model presentations (GLM)	**Probability of giving an alarm call**						
		(Intercept)		-1.96±1.70			
		Sex (Female)	Male	2.44±1.02	**1**	**6.86**	**0.0088**
		Model (Adult)	Juvenile	-0.56±1.06	1	0.29	0.59
		Distance		0.08±0.11	1	0.53	0.47
(f) Model presentations (GLM)	**Probability of fleeing**						
		(Intercept)		-0.39±1.35			
		Sex (Female)	Male	-0.68±0.96	1	0.50	0.48
		Model (Adult)	Juvenile	1.33±0.96	1	2.03	0.15
		Distance		0.07±0.09	1	0.55	0.46

Table 2.3. *Outcomes of models to investigate the effects of bird sex on a) the probability of giving an alarm call, b) the number of alarm elements produced, c) the proportion of calls given when perched, d) the time spent perching, e) the probability of fleeing to the model predator, and f) the effects of bird sex on the probability of giving an alarm call to the model predator. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

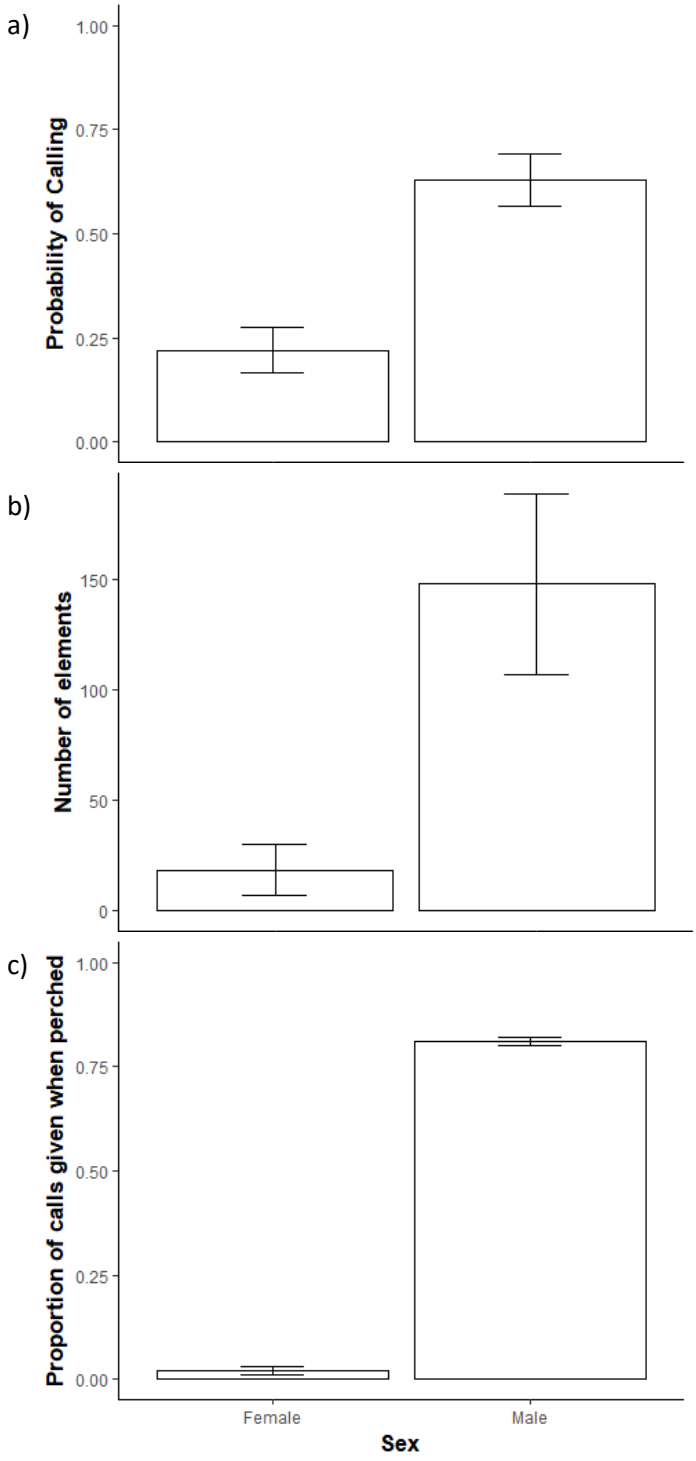


Figure 2.6. *The effect of sex on: a) The probability of producing at least one alarm call during a focal session, b) the number of elements given during focal sessions in which at least one alarm call was produced, and c) the proportion of alarm calls given when perched. Raw data shown. Columns represent means. Bars represent standard errors. n = 10 females, 10 males.*

Time Budget Observations

Male honeyeaters spent more time perched than females. Males spent around 40 minutes perching per hour, which is more than double the amount of time females spent perched during the focal sessions (Table 2.3d; Fig. 2.7). This suggests that males were more likely to see potential aerial threats than females.

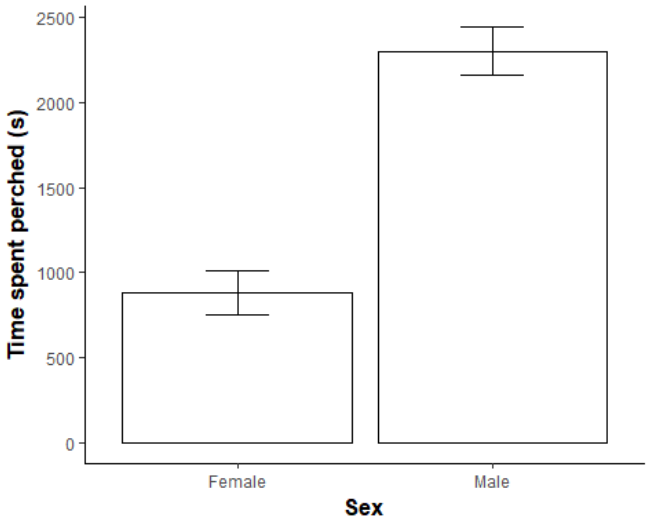


Figure 2.7. *The effect of sex on the time spent perching during 1-hr focal sessions. Raw data shown. Columns represent means. Bars represent standard errors. n = 8 females, 8 males.*

Model Presentations

When gliding model predators were presented to perched birds, male honeyeaters were three times more likely than females to give an alarm call when presented with a gliding model predator (Table 2.3e; Fig. 2.8a, p 50). However, both sexes were equally likely to flee to the model, implying that it was equally visible to both sexes (Table 2.3f; Fig. 2.8b). The model type and the distance at which the model was presented did not affect either the fleeing or calling response (Table 2.3e-f).

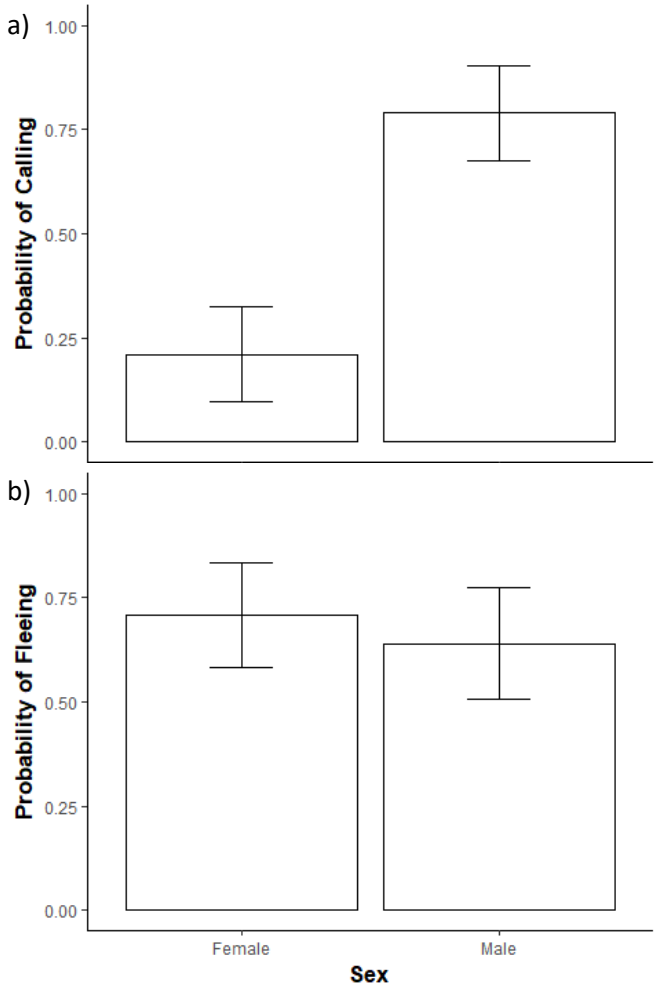


Figure 2.8. *The effect of bird sex on a) the probability of calling, and b) the probability of fleeing to a gliding model predator. Raw data shown. Columns represent means. Bars represent standard errors. n = 14 females, 14 males.*

2.5 Discussion

In this chapter, I show that New Holland honeyeaters often give a distinct whistle call in response to aerial predators, which is consistent with previous work concluding that it is an aerial alarm call. The production of this aerial alarm call is strongly sex-biased, with male honeyeaters producing the majority of the calls. While there are ecological differences between males and females, these appear not to be solely responsible for the bias in alarm production.

Previous work on the alarm calls of New Holland honeyeaters suggested that they use the whistle call as an aerial alarm call, but these studies were based on very small sample sizes or did not include detailed observations (Jurisevic & Sanderson, 1994b; Magrath et al., 2009a; Rooke & Knight, 1977). For example, in Magrath et al. (2009a), they recorded 8 calling bouts during the 11-hr study

period and identified only 4 prompts, whereas Jurisevic and Sanderson (1994) reported 9 out of 12 whistle call bouts as having been prompted by the sudden appearance of human. In this study, I found that over 80% of the 57 identified prompts were in flight and around 70% were predators, corroborating the idea that the whistle call is used to signal the presence of aerial predators. Supporting this view, gliding model predators prompted these aerial alarm calls in New Holland honeyeaters, and playbacks of these calls prompt fleeing responses in honeyeaters and other species, which have a similar response to conspecific aerial alarm calls (Magrath et al., 2009a, 2009b).

Context-specific alarm calls are not uncommon in mammals and birds (Macedonia & Evans, 1993; Suzuki, 2016). The advantage of calls that are associated with a particular class of predators is that they enable receivers to take appropriate evasive action. This was first demonstrated in birds in a study that found male domestic chickens, *Gallus gallus domesticus*, give distinct alarm calls to aerial and ground predators, and that playbacks of each call elicits a threat-appropriate response: alarms to aerial predators prompted individuals to flee or crouch and look upwards, whereas playbacks of the calls given to ground predators resulted in individuals scanning horizontally and standing in an erect posture (Evans et al., 1993). Threat-specific alarm calls can also improve detection of threats. Japanese tits, *Parus minor*, that heard their snake-specific alarm calls were more responsive to snake-like visual stimuli (Suzuki, 2018). A study on Siberian jays, *Perisoreus infaustus*, found that individuals that were warned by alarm calls of an aerial attack escaped more rapidly and showed greater survival than individuals that were not warned (Griesser, 2013), demonstrating the value of aerial alarm calls.

Across all observation sessions carried out in this study, I found consistent sex differences in the behaviour of the New Holland honeyeaters. Although over 80% of the observed callers in the initial study on alarm context were male, this result could potentially have arisen as a side-effect of other differences or a skewed sex ratio. In several species, male birds have been reported to forage, and engage in more activities, higher in the canopy than females, which could result in males being more visible to the observers (Fogg et al., 2013; Greig-Smith, 1983; Morimoto & Wasserman, 1991; Sodhi et al., 1995). Furthermore, New Holland honeyeaters have been reported to have a male-biased sex ratio

amongst adults (Higgins et al., 2001). However, I found males were still more likely to give alarm calls than females when I conducted focal observations on individuals of both sexes, suggesting that the differences in call production were not an artefact of observer bias or population sex ratio.

While male-biased song production is commonly reported in the literature on songbirds and song is often deemed to be a sexually dimorphic behaviour, calls are generally considered to be given by both sexes and there are substantially fewer studies detailing sex-biased production of calls (Catchpole & Slater, 2003; Freeberg & Branch, 2013). Mobbing is commonly associated with nest defence and there have been reports of sex differences in this anti-predator behaviour, as males and females can take on different roles during reproductive efforts. For most species where a sex difference in mobbing is described, males have been found to produce more calls (e.g. da Cunha et al., 2017; Freeberg & Branch, 2013; Regelmann & Curio, 1986; Shields, 1984; Winkler, 1992) with only a few exceptions (Griggio et al., 2003; Hobson et al., 1988; Maklakov, 2002; Palleroni et al., 2005). The differential investment in mobbing by the sexes has been attributed to males already assuming responsibility for territory defence (Breitwisch, 1988; Francis et al., 1989; Hyman et al., 2013; Markman et al., 1995; Winkler, 1992), self-advertisement of quality or status (da Cunha et al., 2017; Francis et al., 1989; Freeberg & Branch, 2013; Maklakov, 2002) and mate investment (Krams et al., 2006; Markman et al., 1995; Regelmann & Curio, 1986; Shields, 1984) (Table 2.4, p 54). Consistent with the literature on mobbing, there are only a handful of studies that report sex differences in aerial alarm calling behaviour, all of which describe male-biased alarm production (Alatalo & Helle, 1990; Beani & Dessí-Fulgheri, 1998; East, 1981; Griesser & Ekman, 2005; Gyger et al., 1988; Marler, 1956) (Table 2.4). This suggests that, for these species at least, there could be sex-specific variation in the costs and benefits to giving aerial alarms.

Sex-biased alarm production could arise from sex differences in the likelihood of detecting a predator. Male New Holland honeyeaters spent considerably more time perched than females did during focal observations, spending around 40 minutes of every hour, compared to 15 minutes for females, in a perched position. This considerable investment in vigilance is likely to present males with

better opportunities for predator detection, as indirect evidence indicates that perched birds may be better able to see oncoming predators or may detect them more rapidly than foraging birds (Greig-Smith, 1981; Kaby & Lind, 2003; Radford et al., 2009; Ragusa-Netto, 2002; Ridley et al., 2010). The sex difference in perching time may result from male honeyeaters taking the primary role in defending the territory from conspecific intruders and heterospecific competitors, such that greater opportunities for spotting predators is a byproduct of vigilance against intruders (Paton, 1985; Recher, 1977). Breeding male Florida scrub jays, *Aphelocoma coerulescens coerulescens*, spend more time on sentinel duty than other flock-member classes, and they are most likely to detect a predator and spend the longest time mobbing it (Francis et al., 1989; Hailman et al., 1994). In male grey partridges, *Perdix perdix*, increased investment in vigilance correlated with greater alarm calling and with mating success (Beani & Dessí-Fulgheri, 1998). Vigilance and calling behaviour in partridges were both governed by testosterone levels (Fusani et al., 1997). A similar relationship between alarm calling and vigilance was found in male chickens (Pizzari, 2003). There is some observational evidence from other studies to suggest that male vigilance benefits female survival, rather than enhancing male survival or mate guarding, and could function as an honest signal of quality (Artiss et al., 1999; Fusani et al., 1997; Lou et al., 2017; Squires et al., 2007).

It is possible that the costs and benefits of calling may be different for individuals that are perched in an exposed position and those that are feeding close to cover. Exposed birds may benefit from signaling that they have detected predators, whereas birds in close proximity to cover may seek to escape detection by remaining silent. Indeed, the sole empirical study demonstrating a direct benefit to aerial alarm calling used models that were conspicuously perched (Kareksela et al., 2013), and in the observational study in Belding's ground squirrels, *Spermophilus beldingi*, aerial alarm callers were usually far from cover (Sherman, 1985). However, in New Holland honeyeaters, only males appear to preferentially call when perched, producing around 80% of their alarm calls when perched. Female honeyeaters, on the other hand, rarely gave alarm calls from a perched position.

Hypothesis	Predictions	Alarm Type	Sex that calls more	Strong sexual dimorphism	Species	References
Nepotism	Call more in presence of relatives	Aerial	M	N	European robin	East (1981)
		Ground	M	N	Siberian jay	Griesser & Ekman (2005)
			F	Y	Domestic chicken	Palleroni et al. (2005)
	Sex that shows natal philopatry calls more	Aerial	M	N	Siberian jay	Griesser & Ekman (2004)
		Ground	M	N	Florida scrub-jay	Woolfenden & Fitzpatrick (1986)
	Sex with greater paternity certainty calls more	Ground	F	Y	Yellow warbler	Hobson et al. (1988)
			F	Y	Domestic chicken	Palleroni et al. (2005)
Self-advertisement	Call more in presence of potential mates	Ground	M	Y	19 Brazilian species	da Cunha et al. (2017)
	Sex with greater mating potential calls more	Alarm Song	M	Y	Superb fairy-wren	Langmore & Mulder (1992)
Mate investment	Call more in presence of mate	Aerial	M	Y	Domestic chicken	Karakashian et al. (1988)
			M	N	Red-legged partridge	Zaccaroni et al. (2013)
			M	N	Willow tit	Hogstad (1995)
			M	N	European robin	East (1981)
		Ground	M	N	Great tit	Regelmann & Curio (1986)
	Sex that is more common, or has lower re-mating potential, calls more	Aerial	M	Y	Domestic chicken	Karakashian et al. (1988)
			M	N	Willow tit	Hogstad (1995)
			M	N	New Holland honeyeater	Higgins et al. (2001); this study
			M	N	Red-legged partridge	Nadal et al. (1996); Zaccaroni et al. (2013)
		Ground	M	N	Northern mockingbird	Breitwisch (1988)
			M	Y	Barn swallow	Shields (1984)
			M	N	Great tit	Regelmann & Curio (1986)
			M	N	Scaled quail	Anderson (1978); Brown & Gutiérrez (1980)
Task specialisation	Call more if more vigilant	Aerial	M	N	New Holland honeyeater	This study
			M	N	Grey partridge	Beani & Dessí-Fulgheri (1998)
			M	Y	Domestic chicken	Pizzari (2003)
			M	N	Arabian babbler	Wright et al. (2001)
		Ground	M	N	Florida scrub-jay	Francis et al. (1989)
	Sex responsible for territory defence/sentinel behaviour calls more	Aerial	M	N	New Holland honeyeater	Paton (1985); Recher (1977); this study
			M	N	Arabian babbler	Wright et al. (2001)
		Ground	M	N	Florida scrub-jay	Francis et al. (1989)
			M	N	Tree swallows	Winkler (1992)
			M	N	Scaled quail	Anderson (1978)
			M	Y	Orange tufted sunbird	Markman et al. (1995)

***Table 2.4**. Summary of hypotheses for sex-biased production of alarm calls*

While male honeyeaters appear to be more likely to detect oncoming threats, the model presentation experiment revealed that even when both sexes saw the threat, males were more likely to give alarm calls. The probability of calling for both males and females during the presentations was similar to the probabilities found during the focal observations, suggesting that this difference in the propensity to call may be driving the results. In both a polygamous and a monogamous species of Galliformes, males were found to give significantly more aerial alarm calls than females during model presentations, and in both species the production of alarm calls was linked to testosterone levels (Fusani et al., 1997; Gyger et al., 1988; Palleroni et al., 2005). The male-biased calling appears to constitute a form of mate investment: male domestic chickens increase their alarm calling effort following matings, and both male chickens and male red-legged partridges, *Alectoris rufa*, increase calling in the presence of a female (Beani & Dessí-Fulgheri, 1998; Karakashian et al., 1988; Wilson & Evans, 2008; Zaccaroni et al., 2013). Mate investment has also been proposed as an explanation for sex-biased alarm calling in flocking willow tits, *Parus montanus*, where adult males call less when they cannot see their mates, and in black-capped chickadees, which produce very low amplitude alarm calls (Alatalo & Helle, 1990; Hogstad, 1995; Witkin & Ficken, 1979). As male honeyeaters often select perches near their foraging mates during incubation and brooding (personal observation), their investment in anti-predator behaviours, namely vigilance and alarm calling, could protect their mates from predation. However, the honeyeater aerial alarm calls are considerably louder than those given by the domestic chicken and parids (Wilson & Evans, 2012; Witkin & Ficken, 1979), and can be heard up to 500m away, much further than would be required to communicate with their mates (Higgins et al., 2001). Given the conspicuous nature of the calls, it seems plausible that New Holland alarm calls may serve additional functions beyond warning mates of danger, such as self-advertisement or communicating with predators directly.

In this chapter, I confirm that New Holland honeyeaters produce an alarm call that is associated with the presence of flying predators and show that it is primarily produced by male honeyeaters. Variation in the production of calls according to the sex of the caller is not widely

reported, but it appears that alarm call production can often be skewed towards male callers, regardless of the specific alarm type. There is some evidence to suggest that, like in song production, alarm calling may be controlled by testosterone, a male sex hormone (Catchpole & Slater, 2003; Fusani et al., 1997; Gyger et al., 1988). However, it is not clear from our currently limited understanding of the costs and benefits associated with calling in a dangerous context why there might be different selection pressures on males and females. Future studies should look to defining a unifying framework that would allow us to understand why, and predict when, asymmetric call production might arise.

Chapter 3

How an alarm signal encodes for when to flee and for how long to hide

3.1 SUMMARY

Paradoxically, many species indicate danger in their alarm calls by using multi-element calls in which a larger number of elements signals greater danger. While including more elements should aid signal detection, this system is nevertheless puzzling: multi-element calls necessarily take longer to produce than single-element calls, which compromises rapid responses. Here, I report a solution to this problem. I used both observations and presentations of model predators and playbacks to determine the mechanisms by which New Holland honeyeaters encode urgency information in their alarm calls to aerial predators and how receivers use this information. During natural encounters with a food competitor, an opportunistic predator and a specialised predator, honeyeaters incorporated more elements in calls given to more dangerous predators. Presentations of model predators confirmed this finding. The type of threat also affected the acoustic structure of the first element of the alarm calls. Playbacks of natural alarm calls revealed that honeyeaters were more likely to flee to calls containing more elements, but detailed video analyses revealed that responses occurred in under a quarter of a second, after hearing only the first 1 – 3 elements. Such rapid information transfer could be vital during a predator attack, and playbacks confirmed that birds need only hear the first element of alarm calls to accurately assess the degree of danger. This begs the question why alarms are comprised of multiple elements, but further playbacks showed that the number of elements determined the time to resume feeding. Together, the results indicate that New Holland honeyeaters have a sophisticated signalling system that enables receivers to make extremely fast decisions about fleeing to alarm calls and to determine for how long to hide. These findings resolve the puzzle of how alarm signals can transfer detailed information about danger rapidly and reliably to conspecifics in the context of life and death.

3.2 INTRODUCTION

Aerial predators on the wing are very dangerous. *Accipiter* hawks hunt at high speeds with attacking velocities ranging from 10 – 25 m/s (Goslow, 1971; Hilton et al., 1999; Kane et al., 2015; Malmiga et al., 2014). As such, potential prey need to be able to react rapidly to information on flying threats because even a delay of 0.5 s could represent a gain of up to 12 m by an attacking hawk. Several studies have found that birds generally take off within 0.5 s of a flying model predator becoming visible (Cresswell et al., 2009; Hilton et al., 1999; Kullberg & Lafrenz, 2007; Quinn & Cresswell, 2005; van der Veen & Lindström, 2000). Even in this short time, the focal birds are able to process the information about the oncoming predator and adjust their escape strategy according to the proximity of the model and the angle of the attack (Lind et al., 2002, 2003).

Individuals may not always detect the approaching predator themselves, leaving them vulnerable to capture (Bohórquez-Herrera et al., 2013; Kenward, 1978; Krause & Godin, 1996). However, vertebrates commonly produce alarm calls that warn others of the presence of danger (Caro, 2005) and can even indicate the specific class of predator (Ausmus & Clarke, 2014; Cunningham & Magrath, 2017; Gill & Bierema, 2013; Grieves et al., 2014; Suzuki, 2015). Discrete call types are often used to differentiate between terrestrial and aerial threats, which have different hunting strategies and require different antipredator responses (Rooke & Knight, 1977; Suzuki, 2016). Terrestrial predators, or perched raptors, are approached and mobbed. Flying threats, on the other hand, require rapid escape if prey are to avoid being captured. Yet little research has been done to look at the speed of responses to aerial alarm calls that warn of flying predators.

As well as signaling about different classes of danger through discrete alarm calls, it is also possible to convey graded information about urgency in a risk-based calling system. The two methods of encoding information can complement each other, providing information about both the type of predator and the degree of danger it poses (Manser, 2001). This is likely to be particularly important for aerial predators, where urgency information encoded in aerial alarm calls can allow receivers to weigh up the costs of an energetically expensive flight to cover against the risk of capture (Nudds &

Bryant, 2000; Rodriguez-Prieto et al., 2008). Birds commonly use a signaling system for both aerial and mobbing threats in which the number of calls or elements (Billings et al., 2017; Courter & Ritchison, 2010; Fallow & Magrath, 2010; Griesser, 2009a; Haftorn, 2000; Templeton et al., 2005; Zachau & Freeberg, 2012), or the rate at which calls are produced (Bell et al., 2009; Curio et al., 1983; Fasanella & Fernández, 2009; Malan et al., 2009; Seoraj-Pillai & Malan, 2014; Shah et al., 2015; Wheatcroft, 2015), increases with greater risk.

Given the speed with which aerial predators can approach, it is surprising that birds encode information in the number of elements. By doing so, receivers need to assess the number of repetitions to determine the degree of danger and so will take a comparatively long time to respond (Leavesley & Magrath, 2005). This delay will be even greater for more dangerous threats because they receive longer, multi-element calls (Leavesley & Magrath, 2005). It therefore seems that alarm systems that signal urgency through call number should also encode the information in some other way to enable receivers to make rapid decisions regarding their escape strategies.

Alarm call structure has been found to vary in relation to urgency in a range of species (Ficken & Witkin, 1977; Malan et al., 2009; Randall & Rogovin, 2002; Shah et al., 2015). Differences in the size or distance of model predators can result in subtle variations in the frequency or temporal parameters of alarm calls. Male fowl, *Gallus gallus*, produce alarm calls that are shorter, louder and have a lower peak frequency in response to closer and faster threats (Wilson & Evans, 2012). Black-capped chickadees, *Poecile atricapilla*, and superb fairy-wrens, *Malurus cyaneus*, both increase the frequency of their alarm elements when faced with greater danger (Fallow & Magrath, 2010; Ficken & Witkin, 1977). However, it is not clear whether receivers attend to these structural differences or simply the number of elements.

For species that encode risk in the number of elements per call, the acoustic structure of the first element of these calls could be of particular importance in enabling individuals to make a rapid assessment of current risk. A study on the alarm calls of Richardson's ground squirrels, *Spermophillus richardsonii*, found that the natural first elements of their alarm calls provoked a stronger response

than subsequent elements, even when the element order was randomised, suggesting that they could serve to alert receivers to the rest of the call (Swan & Hare, 2008). Similarly, the first call given by male fowl in aerial alarm bout differs from subsequent calls in structure by including features that make the caller easier to locate (Bayly & Evans, 2003). Although the position of an element within the aerial alarms of white-browed scrubwrens, *Sericornis frontalis,* has no effect on its acoustic structure, the minimum frequency of all elements increases with predator proximity and element number (Leavesley & Magrath, 2005). The first elements of multi-element alarm systems could thus act as alerting signals or provide essential information on urgency.

In this chapter, I investigated whether New Holland honeyeaters, *Phylidonyris novaehollandiae*, encode risk-based information in their aerial alarm calls and whether receivers attend to this information. These honeyeaters provide a good model for studying the mechanisms by which birds encode sophisticated information in their alarm calls, as they produce loud, multi-element alarm calls in response to flying threats that are attended to by several species in the avian community (Igic et al., 2015; Jurisevic & Sanderson, 1994a; Magrath et al., 2009a; Rooke & Knight, 1977). Furthermore, they flee to cover when presented with playbacks of conspecific aerial alarm calls (Magrath et al., 2009a), allowing for a simple quantification of their response. First, I recorded naturally-prompted alarm calls and presented model predators to determine whether, and how, the birds adjust their calls to signal urgency. I then used a series of playback experiments to first test if honeyeaters respond appropriately to information on risk before investigating which call features affect their escape decisions. I videoed their responses to the playbacks to examine the speed with which they process information about danger.

3.3 METHODS

Study site and species

Data were collected on a colour-banded population of around 70 individual New Holland honeyeaters between June 2014 and July 2017 in the Australian National Botanic Gardens in Canberra, Australia. New Holland honeyeaters are small (20 g), pair-breeding passerines that feed primarily on nectar from flowering plants, as well as arthropods. The botanic gardens comprise 40 ha of both natural and planted vegetation. The birds in the study population were all resident in the gardens and accustomed to the presence of people.

New Holland honeyeaters give two distinct alarm calls (Higgins et al., 2001; Jurisevic & Sanderson, 1994a; Rooke & Knight, 1977): a noisy, broadband "chatter" call that is primarily used in response to terrestrial threats, and an aerial alarm call, which is given to aerial threats and is composed of multiple elements of similar structure (Fig. 3.1a-d, p 64). For the purpose of this study, I focused on the aerial alarm call. Elements are considered to be part of the same call if they are separated by intervals of less than 200 ms, and aerial alarm calls can contain between 1 and 100 elements. Each element consists of a pure, descending whistle of approximately 33 ms in length. The elements are loud, with an amplitude of about 70 dB at 6 m (Magrath et al., 2009a), and relatively low in pitch with a peak frequency of 3.5 kHz.

Statistical Analyses

All statistical analyses were carried out in R version 3.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Linear models and general linear models were carried out using the lm() and glm() functions, respectively. The linear discriminant function analysis was generated using the lda() function of the MASS package, and the stepwise variable selection was carried out using the stepclass() function of the klaR package (Ripley et al., 2017; Weihs et al., 2005). Generalised linear mixed effects models (GLMMs) were constructed with binomial error distributions and logit link functions, using the glmer() function of the lme4 package (Bates et al., 2016). I constructed the linear mixed effects models (LMMs) with normal error distributions and identity link functions, using the

lmer() function of the lme4 package (Bates et al., 2016). I carried out pairwise comparisons using the glht() function of the multcomp package (Hothorn et al., 2008). In all cases, the full model with all terms of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance.

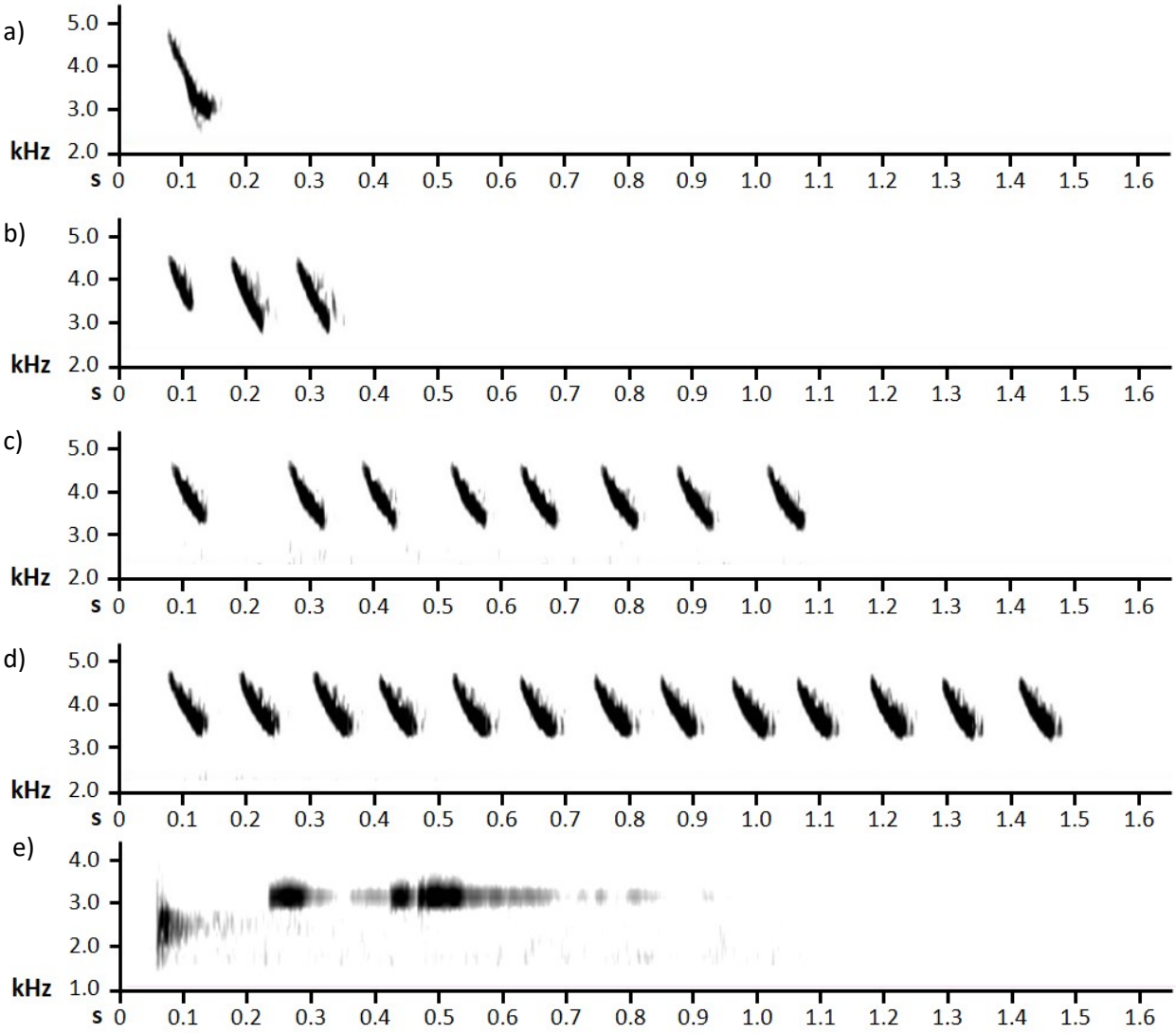


Figure 3.1. *Spectrograms showing examples of a) 1-, b) 3-, c) 8-, d) 13-element honeyeater alarm calls, and e) crimson rosella control call. All alarm calls recorded from the same individual. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz.*

3.4 PRODUCTION OF ALARM CALLS

Natural observations methods

In order to determine whether honeyeaters encode urgency in the number of elements and acoustic structure of their aerial alarm calls, I recorded the alarm calls given during natural encounters with predators and other threats between 2014 and 2017. Recordings were made using Marantz PMD70 and PMD661 MK II solid-state digital recorders with sampling rates of 44.1 kHz and 16 bits, and a Sennheiser ME66 shotgun microphone. The recording equipment was attached to my shoulder and recorded continuously while the birds were followed at a distance of 10 – 20 m. Where possible, the distance between the microphone and the calling bird, the identity of the calling individual and the probable prompt were recorded for any alarm calls given.

The three most commonly observed prompts were red wattlebirds, *Anthochaera carunculata*, pied currawongs, *Strepera graculina*, and collared sparrowhawks, *Accipiter cirrhocephalus*. Wattlebirds are abundant in the gardens, and there are about 15 pairs of currawongs (L. Ascah, personal communication) and 2 pairs of *Accipiter* hawks that breed in the botanic gardens each year. These three species represent an increasing intensity of threats, so they were used to look at how the number of elements and element structure varies with danger: wattlebirds are aggressive but non-predatory nectivores that can displace New Holland honeyeaters during competitive interactions over food, currawongs are primarily nest predators but will opportunistically target small adult birds, and sparrowhawks pose the greatest threat, as they principally feed on small birds around the size of New Holland honeyeaters (Higgins et al., 2001, 2006; Marchant & Higgins, 1993).

I generated spectrograms of the recordings using Raven Pro 1.4, a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz. The spectrograms were used to measure the number of elements and their acoustic structure.

Model presentations methods

It is not possible to infer causal relationships from natural observations alone. During observations of natural threat encounters, the type of threat and the distance from the calling honeyeater were confounded. Honeyeaters only called to wattlebirds that were within 5 m, whereas currawongs usually prompted alarm calls from 10 – 15 m away and sparrowhawks were usually over 20 m away from the calling individual (personal observation). Previous work has found that birds can encode information in their alarm calls about either how dangerous a specific type of predator is or how close the predator is (Fallow & Magrath, 2010; Ficken & Witkin, 1977; Leavesley & Magrath, 2005; Templeton et al., 2005). It was therefore necessary to carry out presentations of different model predators at known distances to disentangle the effects of predator type and distance.

I presented 16 colour-banded male New Holland honeyeaters with gliding model predators (Fig. 3.2, p 67) in July 2017. Each bird was presented with the model when they were perched with a clear view, approximately 10 – 15 m from the thrower, and their vocal response was recorded with a Marantz PMD661 MK II solid-state digital recorder with a sampling rate of 44.1 kHz at 16 bits, and a Sennheiser shotgun microphone. If the bird appeared not to detect the model predator, the presentation was repeated later in the day. Models were thrown such that they flew past the focal bird, rather than directly towards them. However, model trajectories varied unpredictably on every throw. One of the gliding model predators was made out of foam cut with hot wire and was painted to resemble an adult collared sparrowhawk. The other model was made from both foam and balsa wood and painted to look like a pied currawong. Both models were life-sized. Only one exemplar of each model type was presented, but the flight paths of the models varied across presentations, so the exact stimulus birds received would not have been identical. Each bird was presented with both models, receiving only one model presentation per day. Half the birds received the sparrowhawk model first and half received the currawong first. Recordings were analysed in Raven Pro 1.4 (see above).

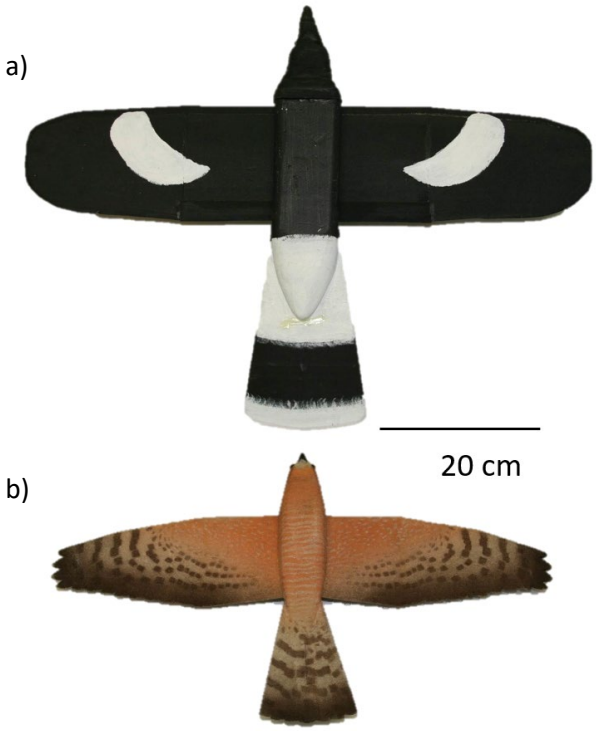


Figure 3.2. *Ventral view of life-sized gliding model predators resembling a) pied currawong and b) collared sparrowhawk. Photographs by Rob Magrath.*

Statistical Analyses

a) Number of elements

I counted the number of elements given per alarm call during natural encounters with wattlebirds, currawongs and sparrowhawks. I only included encounters for which I knew the recording distance and the identity of the calling honeyeater, resulting in a data set of 102 calls given to 57 prompts by 26 birds. If a greater number of elements is associated with a more dangerous predator, birds should include more elements in calls given to sparrowhawks than to wattlebirds, and currawongs should receive an intermediate number of elements.

The model presentations allowed me to isolate the effect of model type, independently of distance, on the probability of birds giving an alarm call and on the number of elements included per call. I recorded whether or not the focal bird gave an alarm call. For the birds that did call, I counted the number of elements given per alarm. If a greater number of elements indicates a more dangerous

predator, the sparrowhawk model should prompt calls containing more elements than the currawong model.

I used linear mixed effects models to look at how the type of threat affects the number of elements in an alarm call during natural encounters and model presentations. The number of elements per call was log-transformed to improve the fit before being entered as the response variable into the model. The type of threat was entered as a fixed effect and the identity of the calling bird was entered as a random effect. For the natural observations, where individual threats sometimes prompted multiple calls, the threat identity was also included as a random effect. For the model presentations, the order in which the model predators were presented and the distance at which they were presented were also included as fixed effects.

To look at the probability of giving an alarm call in relation to which model was presented, I used a generalised linear mixed effects model. The probability of calling was entered as the response variable. The type of model, the distance at which it was presented and the order in which it was presented were entered as fixed effects and the identity of individual birds was included as a random effect.

b) Acoustic structure of the first element

As birds need to show rapid responses to attacking hawks, I hypothesized that the first element of a honeyeater alarm call would convey urgency information. I recorded the duration (s), minimum frequency (Hz), maximum frequency (Hz), peak frequency (the frequency at maximum amplitude; Hz), and frequency range (Hz) of the first element of alarm calls given during natural encounters with wattlebirds, currawongs and sparrowhawks. I used semi-automated measures in Raven Pro that are robust to variations in the manual placement of the selection boxes, as measures are calculated dividing each selection into two intervals that contain 95% and 5% of the energy (Charif et al., 2010). I only included encounters for which I knew the recording distance and the identity of the calling honeyeater, resulting in a data set of 102 elements given to 57 prompts by 26 birds. If the first element of alarm calls encode urgency, element structure should differ between calls given to

sparrowhawks, currawongs and wattlebirds. However, if the first element merely acts as alerting signal, there should be no difference between the different threats.

Unfortunately, the model predators did not prompt a sufficient number of alarm calls (5 calls to the currawong model, 11 calls to the sparrowhawk model) to analyse the acoustic structure of the first alarm element given to the two types of model. This means that any differences observed in the natural data could potentially reflect threat proximity, rather than threat type.

I used linear mixed effects models to examine the effect of threat type on the acoustic structure of the first element of alarm calls. The acoustic measures were entered as the response variables in separate linear mixed effects models. The threat type and the recording distance were entered as fixed effects. To control for any effects the number of elements within the call could potentially have on the acoustic structure of the individual elements, the number of elements was also included as a fixed effect in the model. The identity of the bird and the specific prompt were entered as random effects.

A cross-validated linear discriminant function analysis was performed to establish whether the first elements given to wattlebirds and sparrowhawks could be discriminated by their acoustic structure. I carried out backwards and forwards stepwise variable selection (stepclass) to determine which of the five acoustic measures were most discriminating.

Results

a) Number of elements

Honeyeaters produced alarm calls with higher numbers of elements per call in response to natural encounters with more threatening prompts (Table 3.1a, p 70; Fig. 3.3a, p 71). Birds included twice as many elements per alarm call in response to sparrowhawks than to currawongs (Tukey's test: $z = 2.72$, $p = 0.018$) and over three times as many in response to sparrowhawks than to wattlebirds (Tukey's test: $z = 3.89$, $p < 0.001$).

Honeyeaters were more than twice as likely to give an alarm call in response to the presentation of the sparrowhawk model than to the currawong model (Table 3.1b; Fig. 3.3b)

Furthermore, birds that called gave over double the number of elements per call to the sparrowhawk than to the currawong model (Table 3.1c; Fig. 3.3c), and the number of elements given to each model type were similar to those prompted by natural predator encounters with those threats. This suggests that the number of elements in honeyeater alarm calls conveys the degree of danger posed by a particular type of predator.

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Natural observations (LMM)	**Number of elements**						
		(Intercept)		0.96±0.25			
		Threat (Wattlebird)	Currawong	0.29±0.37	**2**	**15.40**	**0.0005**
			Sparrowhawk	1.32±0.34			
	Random term	*Prompt - variance*		0.21			
		Bird ID - variance		0.17			
(b) Model presentations (GLMM)	**Probability of alarm calling**						
		(Intercept)		-1.34±0.94			
		Model (Currawong)	Sparrowhawk	1.97±1.12	**1**	**5.09**	**0.024**
		Order (First)	Second	0.71±0.89	1	0.69	0.41
	Random term	*Bird ID - variance*		0.94			
(c) Model presentations (LMM)	**Number of elements**						
		(Intercept)		7.45±3.15			
		Model (Currawong)	Sparrowhawk	3.79±1.98	**1**	**4.27**	**0.039**
		Order (First)	Second	-1.39±1.95	1	0.89	0.35
	Random term	*Bird ID - variance*		70.34			

Table 3.1. *Production of Alarm Calls: Number of elements. Outcomes of linear mixed effects models (LMM) and generalised linear mixed effects model (GLMM) to investigate the effects of a) threat type on the number of elements given per call, b) model type on the probability of alarm calling and c) model type on the number of elements given per call. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

b) Acoustic structure of the first element

The first elements of honeyeater alarm calls given during natural encounters with sparrowhawks, currawongs and wattlebirds differed in the frequency parameters of their acoustic structure (Table 3.2, p 72; Fig. 3.4, p 73). The first elements of calls given to sparrowhawks had lower minimum frequencies than those from calls given to currawongs (Tukey's test: z = -3.22, p = 0.004) or wattlebirds (Tukey's test: z = -4.80, p <0.001). Elements from sparrowhawk-prompted calls also had lower maximum frequencies than elements from calls prompted by currawongs (Tukey's test: z = -2.64, p = 0.023) or wattlebirds (Tukey's test: z = -3.31, p = 0.003). Finally, the first elements of calls

given to sparrowhawks had lower peak frequencies than elements from calls to wattlebirds (Tukey's test: z = -3.42, p = 0.002).

Stepwise variable selection identified the maximum frequency as the most discriminating parameter. The cross-validated linear discriminant function assigned 73% of the first elements to the correct threat based on their maximum frequency.

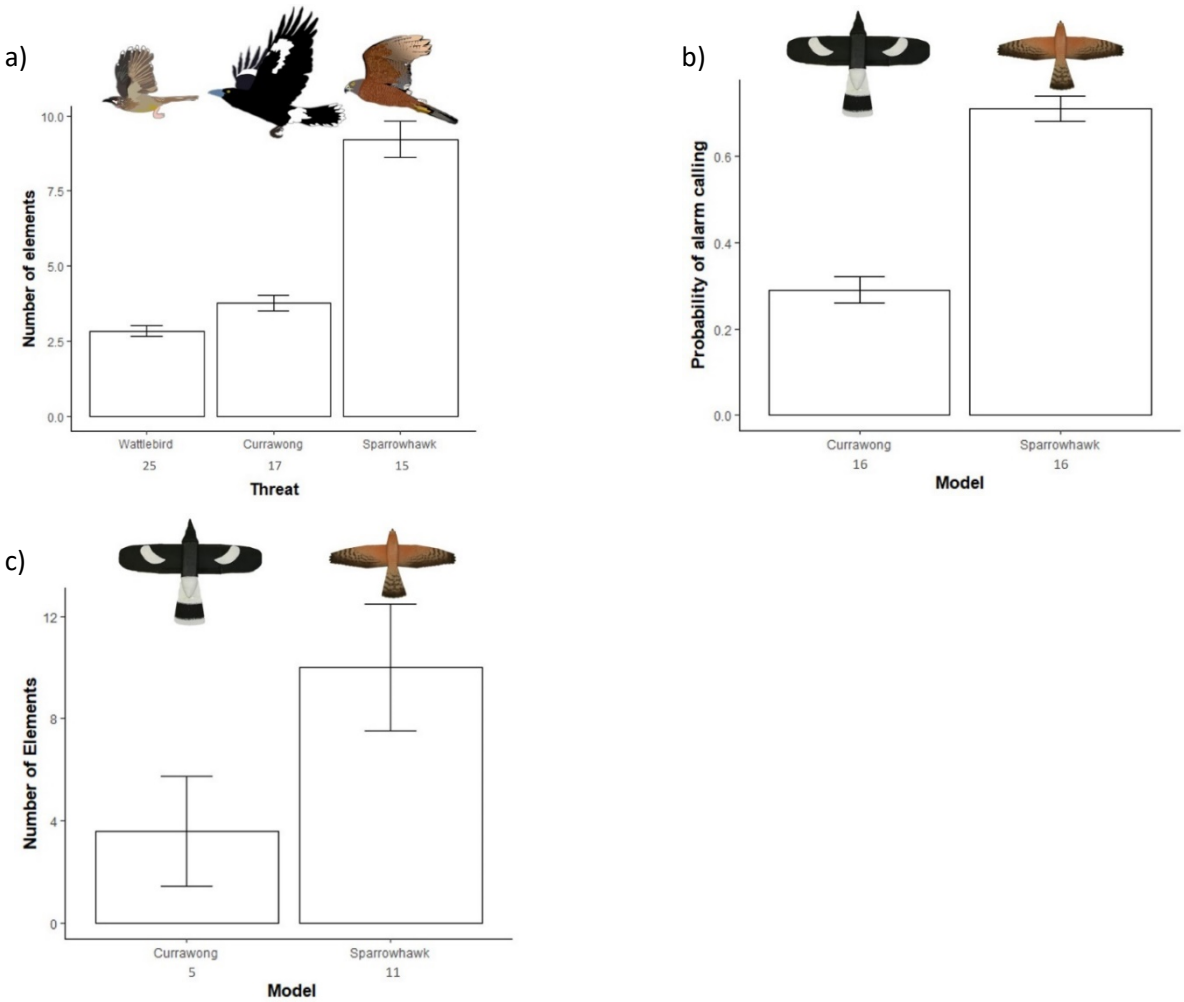


Figure 3.3. *a) Number of elements given per alarm call in natural encounters with different threats, b) probability of giving an alarm call to experimental presentations of different models, and c) number of elements given per alarm call to different models. Fitted values shown. Columns represent means. Bars represent standard errors. Sample sizes shown below columns.*

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Duration (LMM)	**Duration**						
		(Intercept)		-3.52±0.11			
		Threat (Wattlebird)	Currawong	0.08±0.06	2	6.95	0.03
			Sparrowhawk	0.13±0.06			
		Recording distance		0.01±0.01	1	0.36	0.55
		Number of elements			**32**	**65.785**	**0.0004**
	Random term	*Prompt - variance*		0.01			
		Bird - variance		0.04			
(b) Minimum frequency (LMM)	**Minimum frequency**						
		(Intercept)		3444.10±77.85			
		Threat (Wattlebird)	Currawong	-67.71±44.67	**2**	**23.27**	**<0.0001**
			Sparrowhawk	-223.06±46.52			
		Recording distance		0.57±7.16	1	0.08	0.77
		Number of elements			32	47.36	0.04
	Random term	*Prompt - variance*		1684			
		Bird - variance		12153			
(c) Maximum frequency (LMM)	**Maximum frequency**						
		(Intercept)		4436.78±87.32			
		Threat (Wattlebird)	Currawong	-36.93±66.02	**2**	**13.01**	**0.0015**
			Sparrowhawk	-241.78±73.13			
		Recording distance		0.57±7.16	1	0.75	0.39
		Number of elements			**32**	**69.66**	**0.0001**
	Random term	*Prompt - variance*		27225			
		Bird - variance		0			
(d) Peak frequency (LMM)	**Peak frequency**						
		(Intercept)		-3900.66±105.09			
		Threat (Wattlebird)	Currawong	-96.54±73.91	**2**	**16.61**	**0.0002**
			Sparrowhawk	-255.71±74.73			
		Recording distance		-10.33±10.16	1	1.59	0.21
		Number of elements			32	32.00	0.47
	Random term	*Prompt - variance*		0.00			
		Bird - variance		0.00			
(e) Frequency range (LMM)	**Frequency range**						
		(Intercept)		967.03±104.06			
		Threat (Wattlebird)	Currawong	20.06±67.88	2	2.11	0.35
			Sparrowhawk	-81.39±71.84			
		Recording distance		-3.72±9.94	1	0.13	0.72
		Number of elements			**32**	**60.92**	**0.0015**
	Random term	*Prompt - variance*		16987			
		Bird - variance		20083			

Table 3.2. *Production of Alarm Calls: Acoustic Structure. Outcomes of linear mixed effects models (LMM) to investigate the effects of threat type on the a) duration, b) minimum frequency, c) maximum frequency, d) peak frequency, and e) frequency range of the first element of alarm calls. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model (Bonferroni correction applied: p < 0.003).*

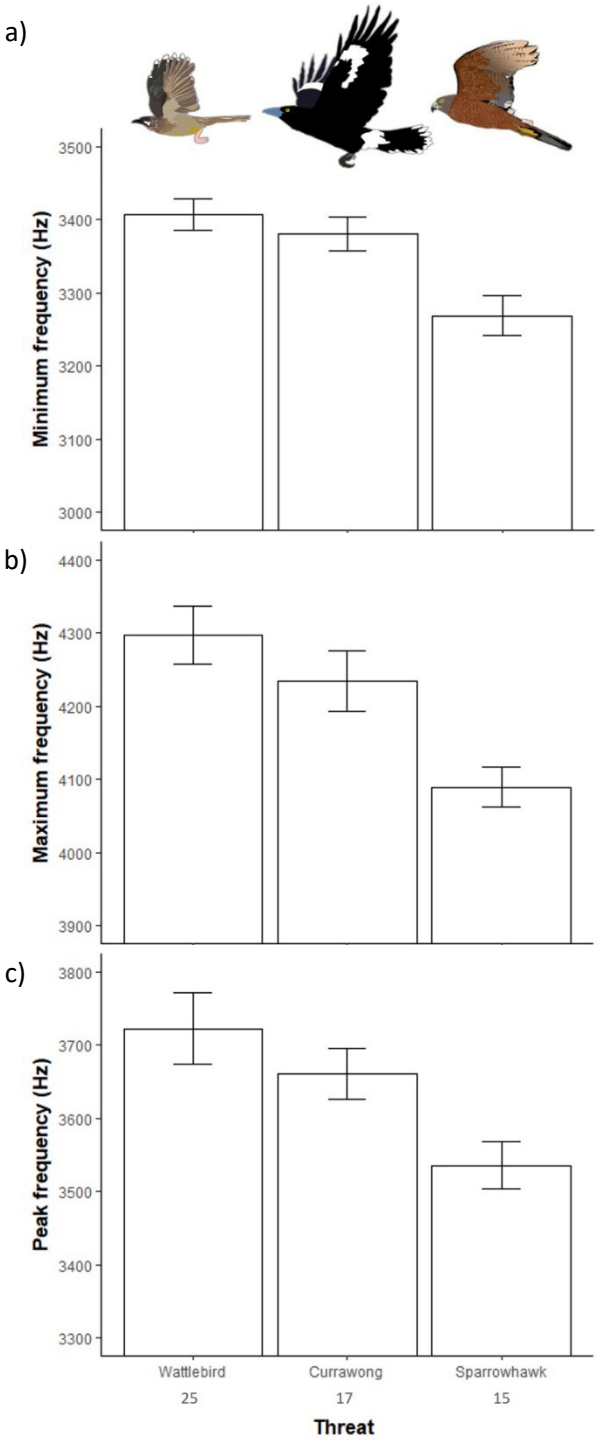


Figure 3.4. *Effect of natural encounters with three threats on a) minimum frequency, b) maximum frequency, and c) peak frequency of the first element of alarm calls. Raw data shown. Columns represent means. Bars represent standard errors. Sample sizes shown below columns.*

3.5 RESPONSE TO PLAYBACKS OF ALARM CALLS

General playback methods

I conducted three playback experiments on colour-banded New Holland honeyeaters between October and December 2015. All playbacks were prepared in Raven Pro 1.4. Each playback set consisted of four New Holland honeyeater alarm calls and the contact calls of crimson rosellas, *Platycercus elegans*, as a neutral control (Fig. 3.1e). The honeyeater alarm calls were chosen to represent a range of element numbers. All alarm calls within a set came from the same individual. Sounds below the frequency of the calls were filtered out, by 2 kHz for the alarm call playbacks and 1.5 kHz for the control calls. Playbacks were transferred as wave files to a Roland R-09HR and were broadcast via a custom-made amplifier and a Peerless speaker. The speaker was attached to my waist, giving an approximate height of 1 m. They were calibrated to 70 dB at 6 m, which is within the natural range for both types of call. Responses to all playback presentations were recorded using a Panasonic HC-V770M camcorder filming at 50 frames per second at 1920x1080p, which was supported by a Wizmount CU2pack over my shoulder.

Within each experiment, 12 unique playback sets were presented to 24 New Holland honeyeaters, 12 male and 12 female. Each set was therefore used twice, once for a male and once for a female honeyeater. As I did not have sufficient samples of alarm calls from the same individual to different threats, I instead used the number of elements as a proxy for urgency and chose a range of element lengths to represent varying urgency. Each bird received all playbacks within a set. Playback order was randomised within a blocked design to minimise order effects. Birds were presented with the sounds when foraging on flowers. Playbacks were carried out a minimum of five minutes apart and there was a gap of at least five minutes following any natural alarm call. Playbacks were presented from a distance of 7 – 10 m.

The video recordings of the responses were subsequently analysed frame-by-frame using Adobe Premier Pro and QuickTime. After recording the frame number of the playback onset, the soundtrack was removed to enable blind scoring. The response of the bird was scored as either an

immediate flee to nearby cover (1), which is the most urgent response, or not (0). The video analysis allowed me to record the latency to respond, which was measured as the time from the onset of the playback to the time when the birds initiated a response, generally starting with a rapid head movement or raising of the wings. I also recorded the duration of the response, which was measured as the time from the onset of the response to the time when the birds resumed foraging or departed the feeding area.

Playback experiments

a) Natural playbacks

In the first experiment, each set consisted of 5 treatments: 1-, 3-, 8-, and 13-element natural honeyeater alarm calls to represent a range of urgency, and the contact calls of crimson rosellas as a neutral control. This allowed me to determine the response to natural variation in conspecific alarm calls.

b) First element playbacks

In the second experiment, I presented birds with only the first element of 1-, 3-, 8-, and 13-element alarm calls as well as crimson rosella contact calls as a neutral control. By using only the first elements of the calls, I could test if variation in the acoustic structure of the first element alone provides sufficient information to allow receivers to adjust their responses accordingly.

c) Number of element playbacks

In order to determine the role of the number of elements in an alarm call, the calls were edited and the fourth elements from the eight-element alarm calls were extracted. These extracted elements were then repeated 1, 3, 8 or 13 times with a standardised inter-element interval of 80 ms to create four alarm call treatments, while crimson rosella contact calls were used as a neutral control. This experiment thus enabled me to look at the role of the number of elements without being confounded by the acoustic structure of the elements or their rate of delivery.

Statistical Analyses

As birds never fled to the controls, these were dropped from the analyses. The probability of fleeing to cover was entered as the response variable in a generalised linear mixed effects model. The playback type, the sex of the bird, and the playback order were entered as fixed effects. Where the inclusion of all three factors caused the model to fail to converge, I included only playback type and sex, as this model had the lowest AIC value. The identity of the individual bird and the specific playback set were entered as random effects.

The duration of response was log-transformed to improve fit before being entered as the response variable into a linear mixed effects model. The playback type, the sex of the bird, and the playback order were entered as fixed effects. The identity of the individual bird and the specific playback set were entered as random effects.

Results

a) Natural alarm playbacks

Honeyeaters responded more strongly to natural alarm calls containing more elements. Birds showed a graded increase in fleeing to calls with more elements (Table 3.3a, p 78; Fig. 3.5a, p 77): pairwise comparisons revealed that birds were more than twice as likely to flee into cover in response to 13-element alarm calls than to 1-element (Tukey's test: $z = 3.19$, $p = 0.007$), and 3-element (Tukey's test: $z = 3.53$, $p = 0.002$). Honeyeaters also took longer to resume feeding following calls comprised of more elements (Table 3.3b; Fig. 3.5b). Pairwise comparisons revealed that birds responded for over five times longer to 8-element (Tukey's test: $z = 5.41$, $p < 0.001$) and 13-element alarm calls (Tukey's test: $z = 5.33$, $p < 0.001$) than to 1-element calls. They also showed a longer duration of response to 8-element (Tukey's test: $z = 4.76$, $p < 0.001$) and 13-element calls (Tukey's test: $z = 4.83$, $p < 0.001$) than to 3-element alarm calls.

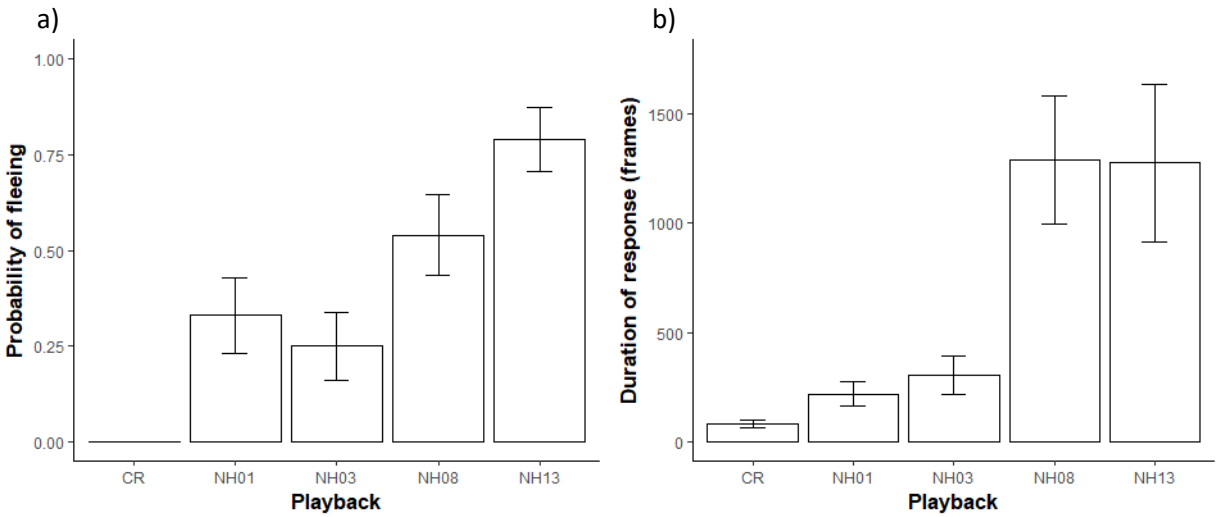


Figure 3.5. *Natural alarm playbacks: a) probability of fleeing to cover, and b) duration of response (50 fps). 1 frame = 20 ms. Raw data shown. Columns represent means. Bars represent standard errors. n = 24 birds. CR = crimson rosella control; NH01 = 1-element honeyeater alarm call; NH03 = 3-element honeyeater alarm call; NH08 = 8-element honeyeater alarm call; NH13 = 13-element honeyeater alarm call.*

Birds responded quickly to the alarm calls (Fig. 3.6, p 79). They showed a visible reaction (looking up or raising their wings) to the calls 100 ms after the onset of the playback (m mean latency to respond ± SEM: 100 ms ± 7, n = 93 responses; 1st element mean duration ± SE: 32 ms ± 0.6, n = 183 calls from 27 individuals). Birds that fled to cover did so extremely rapidly in around a quarter of second (mean time to take off ± SE: 236 ms ± 23, n = 54 flees), which implies that they had decided to flee after hearing only the first 2 - 3 elements of the alarm call (2nd element mean onset ± SE: 126 ms ± 3.3, n = 133 calls from 24 individuals; 3rd element mean onset ± SE: 248 ms ± 5.3, n = 133 calls from 24 individuals). There was no difference between the alarm playbacks in how long it took the birds to react or to flee (Table 3.3c, d), suggesting that birds respond as rapidly to single-element alarms as to multi-element alarm calls. However, when males fled to playbacks, they took much longer to do so than females (Table 3.3d).

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Natural variation (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		-0.35±0.78			
		Playback (1-E)	3-E	-0.63±0.80	**3**	**24.24**	**<0.0001**
			8-E	1.38±0.79			
			13-E	3.22±1.01			
		Sex (Female)	Male	-1.55±0.84	1	3.43	0.06
	Random term	*Bird - variance*		1.76			
		PB set - variance		1.15			
(b) Natural variation (LMM)	**Duration of response**						
		(Intercept)		5.18±0.36			
		Playback (1-E)	3-E	0.16±0.29	**3**	**42.56**	**<0.0001**
			8-E	1.56±0.29			
			13-E	1.57±0.30			
		Sex (Female)	Male	-0.04±0.22	1	0.04	0.83
		Order (First)	Second	-0.49±0.38	4	1.90	0.76
			Third	-0.20±0.33			
			Fourth	-0.19±0.32			
			Fifth	-0.22±0.33			
	Random term	*Bird - variance*		0.03			
		PB set - variance		0.31			
(c) Natural variation (LMM)	**Latency to respond**						
		(Intercept)		1.33±0.17			
		Playback (1-E)	3-E	0.15±0.16	3	3.72	0.29
			8-E	0.22±0.16			
			13-E	0.27±0.16			
		Sex (Female)	Male	-0.05±0.11	1	0.24	0.62
		Order (First)	Second	0.24±0.20	4	3.90	0.42
			Third	-0.03±0.17			
			Fourth	-0.11±0.17			
			Fifth	0.01±0.17			
	Random term	*Bird - variance*		0.00			
		PB set - variance		0.00			
(d) Natural variation (LMM)	**Latency to flee**						
		(Intercept)		1.79±0.24			
		Playback (1-E)	3-E	0.05±0.27	3	5.47	0.14
			8-E	0.43±0.22			
			13-E	0.27±0.21			
		Sex (Female)	Male	0.56±0.21	**1**	**7.40**	**0.007**
		Order (First)	Second	0.12±0.25	4	1.46	0.83
			Third	-0.14±0.21			
			Fourth	0.05±0.19			
			Fifth	-0.05±0.24			
	Random term	*Bird - variance*		0.13			
		PB set - variance		0.01			

Table 3.3. *Response to Alarm Calls: Natural Alarm Playbacks. Outcomes of generalised linear mixed effects models (GLMM) to investigate the effects of playback type on a) the probability of fleeing to cover, b) the duration of response, c) the latency to respond, and d) the latency to flee. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

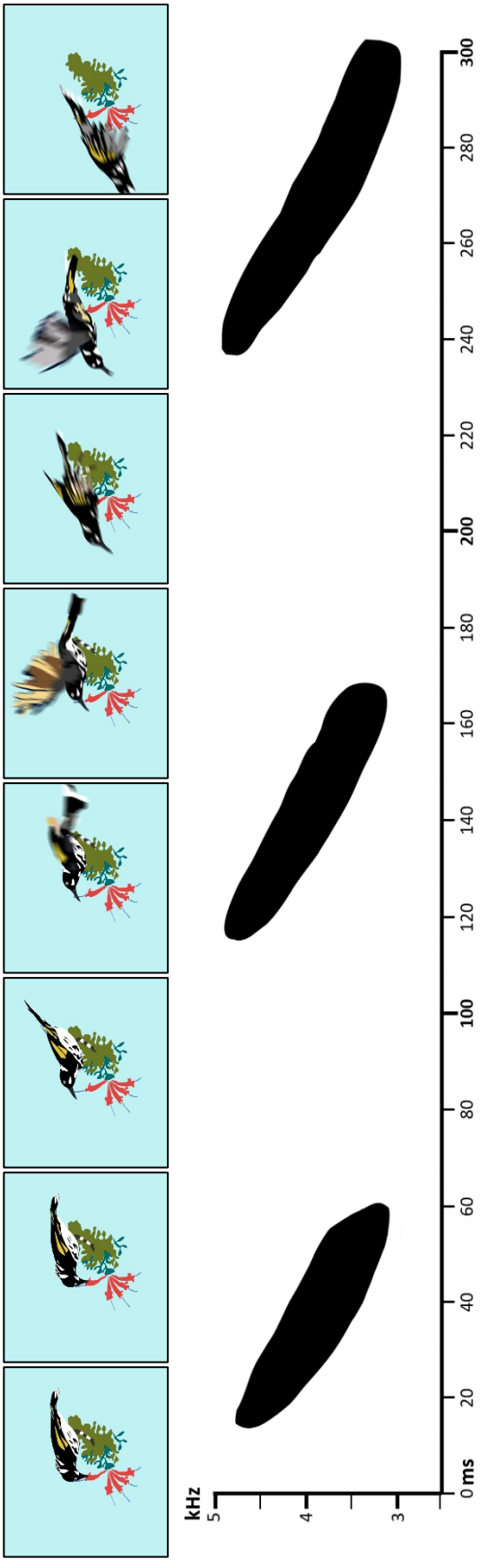


Figure 3.6. *An illustration of the speed of response to playbacks showing the first three elements of a playback. Drawings were created in Adobe Photoshop CC by tracing over reference video frames and spectrograms.*

b) First element playbacks

Consistent with their responses to the natural alarm calls, birds showed stronger fleeing responses to playbacks of first elements that came from calls with more elements (Table 3.4a; Fig. 3.7, p 81). Honeyeaters fled to cover almost three times as often in response to first elements that came from 13-element calls than to elements from 1-element calls (Tukey's test: z = 3.08, p = 0.011). There was no effect of playback on the duration of the response to the calls (Table 3.4b).

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) First elements (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		-1.23±0.84			
		Playback (1-E)	3-E	1.46±0.82	**3**	**12.96**	**0.0047**
			8-E	1.19±0.81			
			13-E	2.84±0.92			
		Sex (Female)	Male	-1.01±0.82	1	1.52	0.22
	Random term	*Bird - variance*		1.94			
		PB set - variance		1.15			
(b) First elements (LMM)	**Duration of response**						
		(Intercept)		4.87±0.27			
		Playback (1-E)	3-E	0.34±0.24	3	5.84	0.12
			8-E	0.18±0.24			
			13-E	0.54±0.24			
		Sex (Female)	Male	-0.40±0.23	1	2.99	0.08
		Order (First)	Second	0.17±0.26	4	2.35	0.67
			Third	0.20±0.25			
			Fourth	0.39±0.27			
			Fifth	0.17±0.28			
	Random term	*Bird - variance*		0.15			
		PB set - variance		0.09			

Table 3.4. *Response to Alarm Calls: First Element Playbacks. Outcomes of linear mixed effects models (LMM) to investigate the effects of playback type on a) the probability of fleeing to cover, and b) the duration of response. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

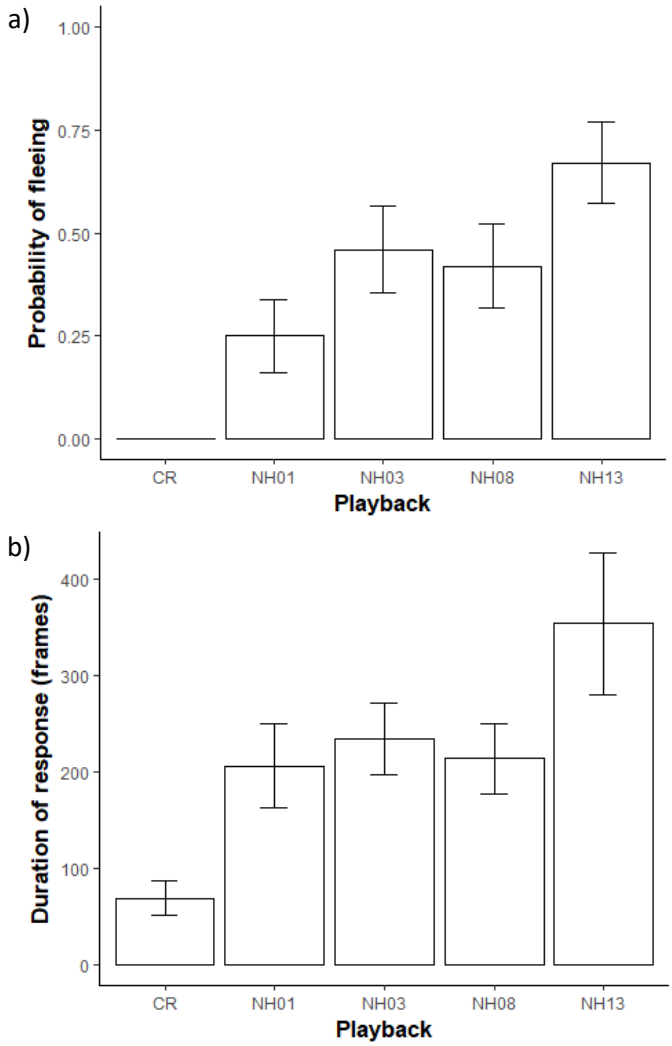


Figure 3.7. *First-element alarm playbacks: a) probability of fleeing to cover, and b) duration of response (50 fps). 1 frame = 20 ms. Raw data shown. Columns represent means. Bars represent standard errors. n = 24 birds. CR = crimson rosella control; NH01 = 1-element honeyeater alarm call; NH03 = first element from 3-element honeyeater alarm call; NH08 = first element from 8-element honeyeater alarm call; NH13 = first element from 13-element honeyeater alarm call.*

c) Number of elements playbacks

Playbacks composed of more elements prompted both greater fleeing responses and longer responses to the playbacks (Table 3.5, p 82). Birds were more likely to flee to calls with more elements (Table 3.5a; Fig. 3.8a, p 82). Twice as many birds immediately fled to cover in response to 13-element than to 1-element calls (Tukey's test: z = 2.70, p = 0.034). Birds also took longer to resume feeding after calls with more elements (Table 3.5b; Fig. 3.8b). Pairwise comparisons revealed that birds responded for longer to 3-element (Tukey's test: z = 2.65, p = 0.04) and 13-element alarm calls (z = 5.18, p < 0.001) than to 1-element calls. They also took longer to return to feeding after a call

composed of 13 elements than calls of 3 elements (z = 2.48, *p* = 0.06) or 8 elements (z = 2.90, *p* = 0.019).

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Number of elements (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		-1.12±0.64			
		Playback (1-E)	3-E	1.82±0.74	**3**	**10.29**	**0.016**
			8-E	1.41±0.73			
			13-E	2.03±0.75			
		Sex (Female)	Male	-0.99±0.50	1	3.63	0.057
	Random term	*Bird - variance*		0.06			
		PB set - variance		0.78			
(b) Number of elements (LMM)	**Duration of response**						
		(Intercept)		5.36±0.37			
		Playback (1-E)	3-E	0.69±0.26	**3**	**24.52**	**<0.0001**
			8-E	0.60±0.25			
			13-E	1.33±0.26			
		Sex (Female)	Male	-0.27±0.28	1	0.96	0.33
		Order (First)	Second	-0.26±0.31	4	7.07	0.13
			Third	-0.52±0.34			
			Fourth	-0.63±0.30			
			Fifth	-0.65±0.31			
	Random term	*Bird - variance*		0.27			
		PB set - variance		0.20			

Table 3.5. *Response to Alarm Calls: First Element Playbacks. Outcomes of linear mixed effects models (LMM) to investigate the effects of playback type on a) the probability of fleeing to cover, and b) the duration of response. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model*

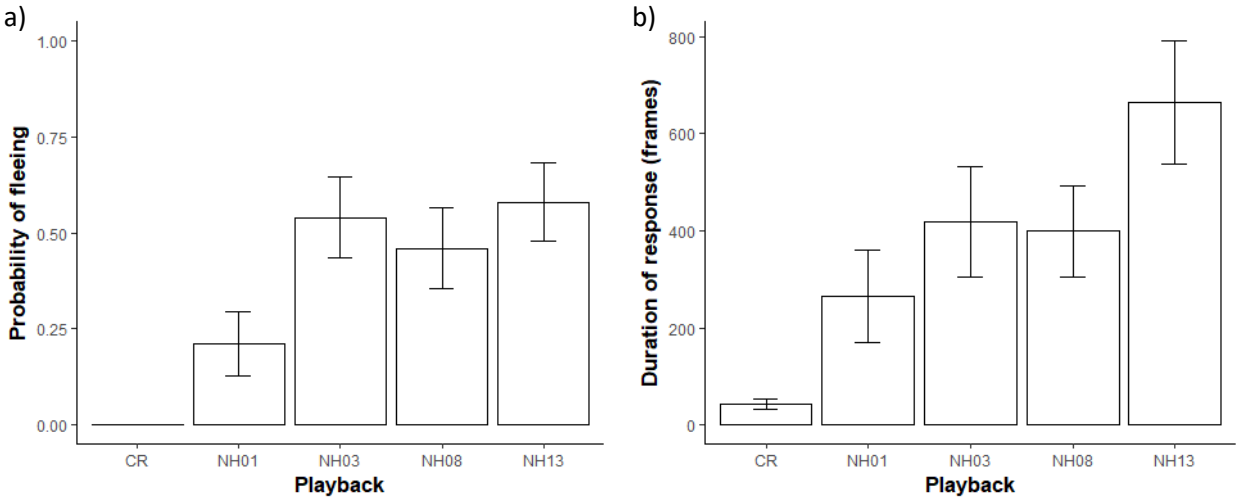


Figure 3.8. *Number of elements alarm playbacks: a) probability of fleeing to cover, and b) duration of response (50 fps). 1 frame = 20 ms. Raw data shown. Columns represent means. Bars represent standard errors. n = 24 birds. CR = crimson rosella control; NH01 = 1-element honeyeater alarm call; NH03 = 3-element honeyeater alarm call; NH08 = 8-element honeyeater alarm call; NH13 = 13-element honeyeater alarm call, where all alarm playbacks consist of the same element repeated to create calls with different numbers of elements.*

3.6 Discussion

In this chapter, I describe a sophisticated alarm calling system that provides detailed information on the current degree of danger. While previous work has shown that risk can be encoded in the number of elements or syllables (Suzuki, 2016), this study reveals a system in which information is transferred by two complementary mechanisms in the form of element number and element structure. This system enables rapid decision-making about fleeing whilst ensuring that the response is maintained for an appropriate duration, therefore resolving the paradox of using longer calls to signal about the threats that require faster responses.

Production of Alarm Calls

New Holland honeyeaters signalled about the degree of risk in their aerial alarm calls by producing higher numbers of elements per call in response to more dangerous threats. Communicating urgency through the number of elements appears to be a common strategy in small birds, in both an aerial (Fallow & Magrath, 2010; Ficken & Witkin, 1977; Haftorn, 2000; Leavesley & Magrath, 2005; Martínez et al., 2017; Zachau & Freeberg, 2012) and a mobbing context (Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010; Billings et al., 2017; Courter & Ritchison, 2010; Griesser, 2009b; Hetrick & Sieving, 2012; Suzuki, 2014). Although encoding greater urgency in a longer, and consequently slower to process, call may seem counterintuitive, this system is likely to be more resistant to mistakes than the reverse. This is because calls composed of more elements must necessarily begin with fewer elements, so a system in which fewer elements signal greater danger could potentially result in many false alarms (Leavesley & Magrath, 2005). There is some evidence that some mammals may encode increased risk in fewer notes or calls; however, receivers either do not appear to use this information or their response has not been tested (Blumstein, 1995; Kern & Radford, 2013; Robinson, 1981).

The structure of the first element of alarm calls may be particularly important for capturing receiver attention (Bayly & Evans, 2003; Swan & Hare, 2008) or for potentially conveying urgency information (Robinson, 1981; Templeton et al., 2005). Consistent with the latter hypothesis, the first element of honeyeater alarm calls showed variation in acoustic structure in relation to threat type. Elements that

were derived from calls given to sparrowhawks were lower pitched than elements from calls to less dangerous threats. Variation in acoustic structure according to alarm urgency has been found in a range of other species (e.g. Bartmess-LeVasseur et al., 2010; Manser et al., 2002; Wilson & Evans, 2012). Chickens give lower and louder calls to more urgent threats and meerkats, *Suricata suricatta*, produce noisier calls when in greater danger (Manser, 2001; Wilson & Evans, 2012). Reducing the frequency of calls enhances transmission over long distances, allowing the sound to reach a wider audience (Naguib & Wiley, 2001). It could be advantageous if honeyeater alarm calls are also directed at the predator to signal it has been detected, as well as communicating with conspecifics. This appears to be the case for the loud calls of primates, which are low-frequency calls that signal predator-type to conspecifics and advertise to ambush predators that they have been spotted (Mitani & Stuht, 1998; Zuberbühler et al., 1997, 1999).

As it was not possible to disentangle the confounding effects of predator type and distance on alarm elements recorded during natural encounters, the acoustic structure of the first elements of honeyeater alarm calls could indicate predator proximity, rather than predator type. If this is the case, closer threats received higher pitched calls. Other small birds vary frequency parameters in association with predator distance or type, increasing the frequency in riskier situations (Fallow & Magrath, 2010; Ficken, 1990; Ficken & Witkin, 1977; Leavesley & Magrath, 2005). Producing higher-pitched calls when the threat is closer may reduce the cost of calling by making the call harder to locate, which may be particularly important in cases where more urgent calls are longer (Marler, 1955; Wood et al., 2000), or it could arise from motivational-structure rules that predict fear-associated sounds will be high frequency (Morton, 1977). Regardless of the specific type of information conveyed by the first element, urgency-related differences in the acoustic structure of the first element of alarm calls should enable species to make swift antipredator decisions.

Response to Alarm Calls

By encoding information in the fine acoustic structure of individual elements, honeyeaters were able to respond extremely rapidly to conspecific alarm calls. Receivers initiated their responses around

100ms after hearing the start of an alarm call and took off from the perch within 250 ms of the onset of the call, rather than waiting to assess the length of the call. This means honeyeaters are able to respond as rapidly to this social information acquired from a conspecific as they would if they had seen the threat themselves (e.g. Quinn & Cresswell, 2005; van der Veen & Lindström, 2000). They appear to be making the decision to flee based on only the first 1-3 elements of the alarm call, which can be confirmed by the fact that their immediate flee responses were comparable when they were presented with only the first element of calls and when they received entire, natural calls.

Consistent with their production of aerial alarm calls, New Holland honeyeaters showed a graded response to playbacks of the calls. They were more likely to flee to cover, and took longer to resume feeding, following presentations of natural calls containing more elements, demonstrating that they pay attention to the degree of danger encoded in conspecific alarms. Honeyeaters, therefore, appear to encode sufficient information within their alarm calls for receivers to make appropriate decisions about whether or not to flee and for how long to hide, which is consistent with work on two sympatric Australian passerines (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). However, the birds showed a similar fleeing pattern when presented with only the first elements of alarm calls, fleeing to cover more frequently to first elements derived from longer calls. This novel finding suggests that honeyeaters can extract detailed information from the first element alone of their multi-element alarm calls to facilitate a rapid anti-predator response.

Variation in the number of elements provides a degree of redundancy, as the call length reinforces the information conveyed by the element structure and should reduce the number of errors made (Johnstone, 1997; Leavesley & Magrath, 2005). One way to increase signal transmission and detectability is to repeat the signal (Wiley, 1994). King penguins, *Aptenodytes patagonicus*, increase the number of syllables per call and the number of calls given when communicating with their mates in windy conditions (Lengagne et al., 1999), and chaffinches, *Fringilla coelebs*, repeat the same song type for longer periods when singing in noisier areas (Brumm & Slater, 2006). Increased signal detection could explain why the birds were twice as likely to flee to all the multi-element calls relative

to single element calls, regardless of the acoustic structure. However, the multiple elements also appear to provide graded information on urgency, as the birds spent more time in cover when presented with longer calls, for both natural alarms and artificial calls made up of the same element repeated. While honeyeaters remained in cover for longer after hearing only the first element of a 13-element call than of a 1-element call, they resumed feeding far more rapidly if this signal was not backed up by additional elements, minimising the temporal cost of fleeing if the caller, or receiver, made an error. A similar result was found in superb fairy-wrens, *Malurus cyaneus*, where individuals spent longer in cover in response to longer alarm calls and fled about twice as frequently to multi-element alarm calls compared to 1-element calls (Fallow & Magrath, 2010; McQueen et al., 2017). For a signal that provides critical information in circumstances requiring split-second decisions, it makes sense to have evolved a call that simultaneously provides complementary information and a measure of redundancy (Johnstone, 1997).

Conclusion

The alarm calls of the New Holland honeyeater represent a sophisticated signaling system that enhances both signal content and efficacy in a potentially fatal context. The dual mechanisms of adjusting both acoustic structure and element number facilitate the flexible transfer of richly detailed information and could potentially allow individuals to simultaneously signal about different aspects of urgency, such as threat type and proximity, within a single call. This neat solution to the issue of delivering both rapid and reliable information in the face of danger raises questions about how widespread this phenomenon is within the avian community at large.

Chapter 4

Honeyeaters value personal information about danger above social information from alarm calls

4.1 SUMMARY

Information about predators can mean the difference between life and death, but prey face the challenge of integrating personal information about predators with social information from the alarm calls of others. As the potential costs are very high in the context of predation, individuals may be expected to rely on social information even if they cannot see the predator themselves, but few studies on anti-predator behaviour consider how these two sources of information may affect decision-making. Here I took advantage of natural variation in the behaviour of New Holland honeyeaters to determine how birds integrate personal and social information in a dangerous context, using presentations of model predators and playbacks experiments together with video recordings to measure behavioural responses. I found that perched honeyeaters reacted more quickly to gliding model predators than feeding birds, suggesting that they have greater access to personal information. Playbacks of alarm calls revealed that perched birds were less likely to flee to cover than foraging birds. The quality of the social information also affected the probability of fleeing for both perched and foraging birds: fewer birds fled when presented with lower quality social information, such as playbacks of more distant alarm calls or alarms from other species with overlapping but not identical threats. These findings show that birds can make flexible decisions about danger by integrating personal and social information, relying on alarm calls when their personal information is limited and valuing their own information over conflicting social information when they have access to both.

4.2 INTRODUCTION

Information about danger is critical for survival. Knowledge about the presence of a predator could potentially mean the difference between life and death (FitzGibbon, 1989; Kenward, 1978; Lingle & Pellis, 2002). Broadly, there are two types of information available to an individual: 1) personal information, which is information gained by an individual interacting directly with its environment, and 2) social information, which comes from observing signals or cues provided by other individuals interacting with the environment (Dall et al., 2005). Personal information is generally seen to be a reliable source of information but can potentially be costly to gather (Giraldeau et al., 2002; Kendal et al., 2009). Social information, on the other hand, can be cheap to acquire but may not necessarily be accurate (Boyd & Richerson, 1988; Laland, 2004; Rieucau & Giraldeau, 2011). The integration of these two sources of information may be particularly important for decision-making in the context of predator avoidance, where the stakes are very high. Both the acquisition of personal information through vigilance and the use of social information in the form of alarm calls represent important aspects of anti-predator behaviour, but studies rarely explicitly consider how these sources may interact with each other. Here I make use of natural variation in the foraging strategies of New Holland honeyeaters, *Phylidonyris novaehollandiae*, to examine how wild birds trade-off conflicting personal and social information about danger.

Individuals are likely to have access to both personal and social information about their environments. When the two sources of information concur with each other, this can result in greater certainty and efficiency in the decisions an individual makes (Cronin, 2013; Czaczkes et al., 2011; Thorogood & Davies, 2016). In the absence of personal information, individuals will rely on social information to choose a feeding patch or nest site (Coolen et al., 2005b; Grüter et al., 2011; Kendal et al., 2004; Templeton & Giraldeau, 1995). However, when the available social information conflicts with prior personal information, individuals need to assess the relative value of the two types of information. The outcome of this decision can depend on the degree of conflict between the two sources (Cronin, 2013), how costly the information is to acquire (Kendal et al., 2004; Templeton &

Giraldeau, 1996; Wray et al., 2012; cf. Grüter et al., 2013), how recently the personal information was acquired (van Bergen et al., 2004), how reliable each type of information is (Dunlap et al., 2016; Heinen & Stephens, 2016), and the quality of the social information (Rieucau & Giraldeau, 2009; Smith et al., 1999).

Foraging animals appear to often disregard conflicting social information when they have access to reliable personal information. For example, experienced bumblebees preferentially selected flower types they personally knew to be profitable over flowers indicated as profitable by social information (Leadbeater & Florent, 2014). However, although the cost of ignoring information is potentially much higher in the context of danger, evidence suggests that individuals may either over- or underestimate the danger when presented with indirect cues of predator presence (Billings et al., 2017; Frechette et al., 2014; Lima & Bednekoff, 2011; Lind et al., 2005; Schneider & Griesser, 2013). For example, yellowhammers, *Emberiza citronella*, that could see a flying sparrowhawk, *Accipiter nisus*, resumed feeding sooner than individuals that could only hear alarm calls prompted by the hawk, evidence that individuals relying on social information can overestimate risk (van der Veen, 2002). On the other hand, sand fiddler crabs, *Uca pugilator*, that only had access to social information about danger, in the form of their neighbours' reactions to an unseen threat, underestimated the danger, retreating into their burrows about 25% of the time, whereas the crabs that were exposed to the threat returned to their burrows over 80% of the time (Wong et al., 2005).

Many vertebrates produce alarm calls to warn others of the presence of a predator, a rapidly transmitted source of social information (Caro, 2005; Endler, 1993). Although alarm call playbacks do not often explicitly test the integration of personal and social information, the experimental design generally requires presenting an alarm call in the absence of a predator, resulting in the potential for conflict between social and personal information on danger (Fischer et al., 2013; Gill & Bierema, 2013; Macedonia & Evans, 1993). Despite this apparent conflict, the majority of individuals do show some sort of response, either by relying entirely on the social information and fleeing immediately or seeking further information by scanning (Aschemeier & Maher, 2011; Cunningham & Magrath, 2017;

Fallow & Magrath, 2010; Furrer & Manser, 2009; Goodale & Kotagama, 2008b; Griesser, 2008; Harris et al., 1983; Hetrick & Sieving, 2012; Igic et al., 2015; Kern et al., 2017; Leavesley & Magrath, 2005; Leger et al., 1979a; Rajala et al., 2003; Ramakrishnan & Coss, 2000b; Ridley et al., 2014; Shriner, 1998).

Even though individuals may show a high level of responsiveness to alarm calls overall, the degree of reliance on that social information can be dependent on several factors. Some alarm calls may be less relevant or reliable than others, reducing receiver responsiveness, because they are given by error-prone juveniles, more distant conspecifics or by heterospecifics with overlapping but not identical predators (Blumstein et al., 2004; Hanson & Coss, 2001; Magrath et al., 2015; Murray & Magrath, 2015). Variation in the internal state, age or position of the receivers could affect how they use the information provided by alarm calls (Grieves et al., 2014; Hollén & Manser, 2006; Kern et al., 2017). For example, male superb fairy-wrens, *Malurus cyaneus*, have conspicuous blue plumage during the breeding season and show stronger responses to alarm calls when they are blue than when they are in their non-breeding brown (McQueen et al., 2017). Even the specific activity in which the receiver is engaged can influence the response: a study on willow tits, *Parus montanus*, found that 15% more birds fled if they were feeding than not feeding in a similar location (Rajala et al., 2012). This is likely because some activities, like foraging, can constrain vigilance and result in a reduction in the amount of personal information available (Beauchamp, 2016; Bohórquez-Herrera et al., 2013; Cords, 1995; Jakobsson et al., 1995).

In this chapter, I used New Holland honeyeaters to determine how individuals integrate personal and social information about danger. The honeyeaters feed on nectar by probing flowers and hawking insects from exposed perches, where they also scan for danger (Higgins et al., 2001; Recher, 1977). This natural variation lends itself to studying information use, as perched birds are likely to have a clearer view of their surroundings and consequently more personal information available to them than foraging birds, which have a restricted view (Beauchamp, 2015; Kern et al., 2017; Kern & Radford, 2014; Radford et al., 2009; Ragusa-Netto, 2002; Rajala et al., 2012). It is not clear from previous research whether perched or foraging birds are at greater risk of being targeted by raptors:

perched birds are generally further from cover and are likely to be alone, both of which have been linked to higher predation risk, but predators have also been shown to select feeding prey (Roth et al., 2006; Whitfield, 2003). I predicted that foraging birds should have more limited personal information about danger and should therefore be more reliant on social information than perched birds. To test this, I presented focal individuals with gliding model predators when they were either perched or foraging to establish whether foraging birds suffered from reduced access to personal information about predators. I then carried out two playback experiments to look at how the position of the focal bird affected its response to social information in the form of alarm calls. In each experiment, I also varied the quality of the social information by presenting them with less urgent information in the form of more distant alarm calls and less relevant information in the form of alarm calls from another species.

4.3 METHODS

Study site and species

Data were collected on a colour-banded population of around 70 New Holland honeyeaters between June 2014 and February 2017 in the Australian National Botanic Gardens in Canberra, Australia. These honeyeaters are small (20 g), pair-breeding passerines that feed primarily on nectar from flowering plants, as well as hawking insects from the air. The birds in the study population were all resident in the botanic gardens, a 40 ha area of both natural and planted vegetation, and accustomed to the presence of people.

New Holland honeyeaters give aerial alarm calls to flying threats (Chapter 2). An aerial alarm consists of a single type of element that can be repeated multiple times. The number of elements in a call is associated with the degree of urgency (Chapter 3). The elements have a peak frequency of around 3.5 kHz and are given at an amplitude of about 70 dB at 6 m (Magrath et al., 2009a).

Model presentation experiment

I conducted model presentations to 20 New Holland honeyeaters, 10 male and 10 female, in February 2017. Two life-sized gliding models, made out of foam cut with hot wire and painted to resemble, respectively, an adult and a juvenile collared sparrowhawk, were used to simulate a predator attack (Fig. 4.1). Each focal bird received two presentations of the same model, once when it was foraging and once when the focal bird was perched. Presentations to the same bird were separated by a minimum of 30 minutes. The models were presented by a thrower standing 15 m from the focal bird, and were thrown such that they travelled past the focal bird at a distance of around 15 m, rather than towards it, at a height of 2-3 m above the ground (Fig. 4.2, p 96). They glided for around 2 s (mean ± SE: 1.85 s ± 0.08) at a speed of about 8.5 m/s (mean ± SE: 8.46 m/s ± 0.34). The location of the focal bird for presentations was chosen to enable the thrower to remain in the same position for both presentations, roughly the same distance away from the focal individual when it was both perched and foraging. Limitations in the set-up of the equipment meant that presentations had to occur when birds were foraging on the same side of the bush as the thrower and when there were minimal obstructions between thrower and bird, which should make any differences between perched and foraging birds conservative.

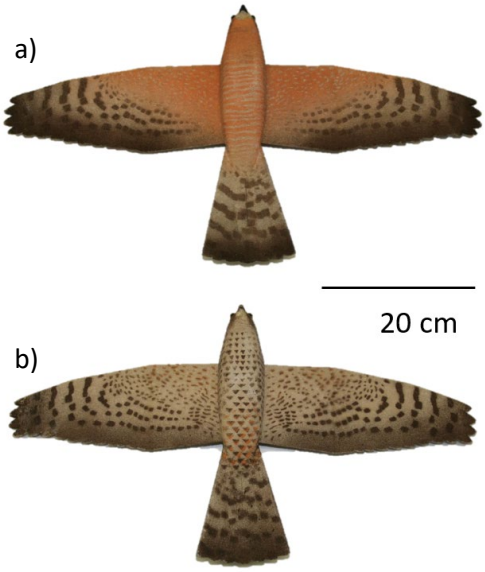


Figure 4.1. *Ventral view of gliding model predators resembling a) an adult and b) a juvenile collared sparrowhawk. Photographs by Rob Magrath. Models made by Alastair Smith.*

The thrower recorded the throws using a Panasonic HC-V770M camcorder on a tripod. An observer stood approximately 5-10 m from the bird and recorded its response using another Panasonic HC-V770M camcorder supported by Wizmount CU2 pack and a Marantz PMD661 MkII solid-state digital recorders with a Sennheiser ME66 shotgun microphone attached to the observer's shoulder. The camcorders filmed at 50 frames per second at a resolution of 1920x1080p. To ensure that the thrower was blind to the position of the bird, the observer used a playback of the words "camera" and "throw" played through a speaker at least 7 m away from the focal bird to signal to the thrower to turn on the camera and to throw the model, respectively. The videos of the throw and of the bird's response were synchronised using the timing of the playbacks and a clicker with an abrupt start and end that was presented after the model had landed. Using the video and sound recordings, I recorded whether the bird detected the model, the time it took for the bird to detect the model, whether the bird fled to cover after detecting the model and whether the bird gave an alarm call. Detection of the model was defined behaviourally as a rapid head turn that oriented the bill towards the model, or a rapid vertical extension of the neck when oriented towards the model, resulting in a head-up movement (Fernández-Juricic et al., 2012; Palleroni et al., 2005; Tisdale & Fernández-Juricic, 2009). The time to detection was measured as the time from when the model left the thrower's hands to when the bird showed one of the above behaviours. Detection was followed by freezing, sleeking, visually tracking the model, alarm calling, fleeing or any combination thereof.

If foraging birds do have limited personal information about danger, they should be slower and less likely to detect the model than perched birds. If their antipredator behaviour is driven instead by differences in the motivation to flee from danger, foraging birds should be less likely to flee, as hungry individuals show reduced responsiveness to danger (Kern et al., 2017; Rajala et al., 2012) and individuals tend to adopt sentinel positions when satiated (Bednekoff & Woolfenden, 2003; Clutton-Brock et al., 1999; Wright et al., 2001a).

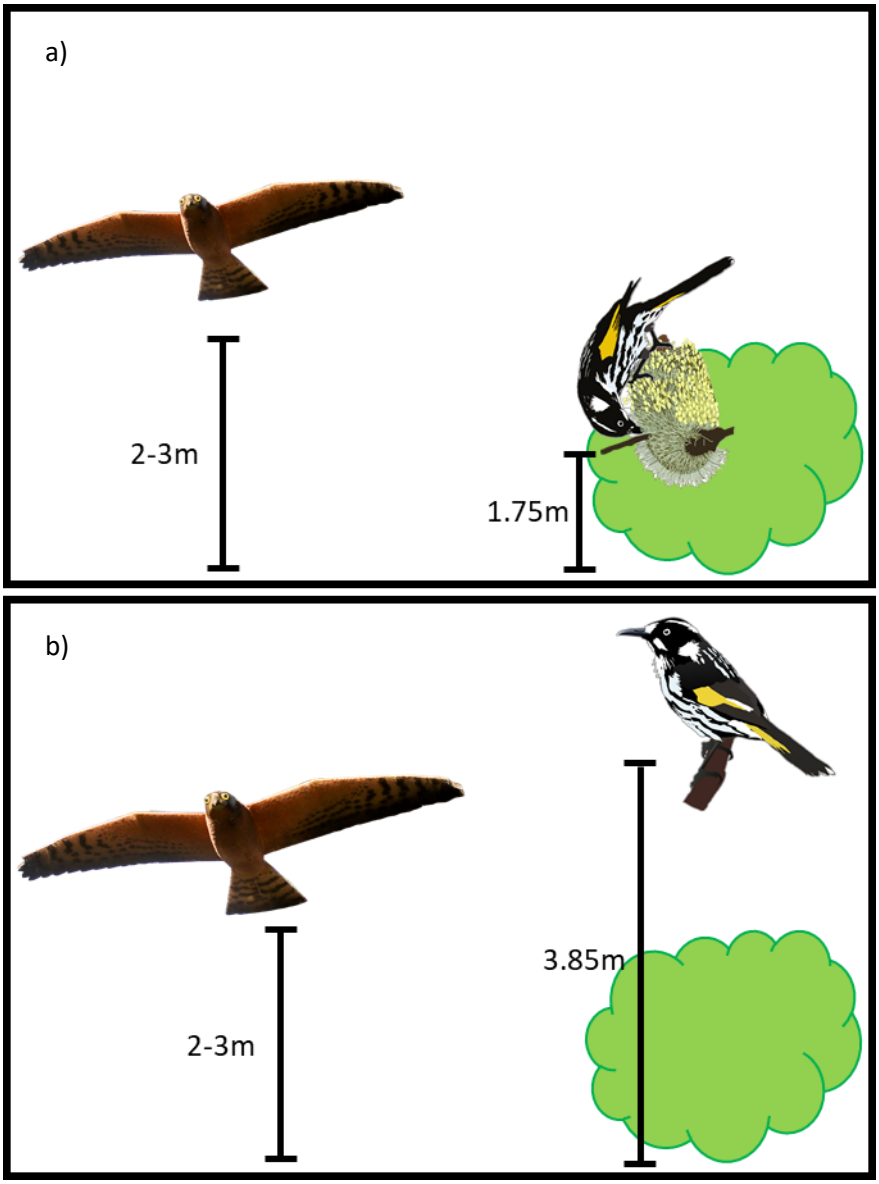


Figure 4.2. *Model presentations: Gliding model sparrowhawks were presented at a distance of approximately 15 m from the focal bird when it was: a) foraging and b) perching. Mean heights of the focal birds and gliding height of the models shown in figure. Images were created in Adobe Photoshop CC, and are not to scale.*

Playback experiments

Recordings of alarm calls

Recordings of natural honeyeater alarm calls were made between June 2014 and August 2015 using Marantz PMD70 and PMD661 MKII solid-state digital recorders with a sampling rate of 44.1 kHz at 16 bits, and a Sennheiser ME66 shotgun microphone. The recording equipment was attached to my shoulder and recorded continuously while the birds were followed at a distance of 10 – 20 m. The distance between the observer and the calling bird and the identity of the calling individual were recorded. Crimson rosella, *Platycercus elegans*, contact calls were opportunistically recorded when

following honeyeaters to be used as control playbacks. White-browed scrubwren, *Sericornis frontalis*, alarm calls were prompted with a gliding model predator. Scrubwren alarm calls prompted by models and by real predators are similar in structure (Magrath et al., 2007).

General playback methods

I conducted two playback experiments on 20 colour-banded New Holland honeyeaters, 10 males and 10 females, between June and August 2015. All playbacks were prepared in Raven Pro 1.4 (Fig. 4.3, p 98). Sounds below the frequency of the calls were filtered out, filtering below 2 kHz for the alarm call playbacks and 1.5 kHz for the control calls. Playbacks were calibrated by recording the playback sounds as well as a reference sound, the amplitude of which was simultaneously measured using a Brüel & Kjær type 2240 sound level meter. Playbacks were transferred as wave files to a Roland R-09HR and were broadcast via a custom-made amplifier and a Peerless speaker attached to my waist, giving an approximate height of 1 m. Responses to playback presentations were recorded using a Panasonic HC-V520 camcorder supported by Wizmount CU2 pack over my shoulder, filming at 25 frames per second at a resolution of 640x360p.

All birds received each playback within a set twice over a period of two days: once when they were foraging on the edge of cover and once when they were perched at least 0.5 m from cover. Playback order within each experiment was randomised within a block design to minimise order effects. Playbacks were carried out a minimum of 5 minutes apart and were only presented after a period of at least 5 minutes in which no alarm calls were produced or predators were nearby. Playbacks were presented from a distance of 7 – 10 m and the immediate response of the bird was scored: 0 – no response, 1 – scan, 2 – scan then flee, 3 – flee but not to cover, 4 – flee to cover. The video recordings of the responses were subsequently analysed blind using Adobe Premiere Pro and QuickTime by recording the frame number of the onset of the playback prior to removing the soundtrack. The response categories were compressed into a binomial scoring system: 0 (0, 1, 2, 3) vs 1 (4) as an indicator of whether the birds immediately fled to cover. By only scoring immediate flees to cover as a success, I could ensure the responses indicated that the birds were relying entirely on

the social information from the alarm calls and not gathering additional personal information before deciding how to respond. The video analysis also allowed me to record the latency to respond, which was measured as the time from the onset of the playback to the time when the birds initiated a response, generally starting with a rapid head movement or raising of the wings.

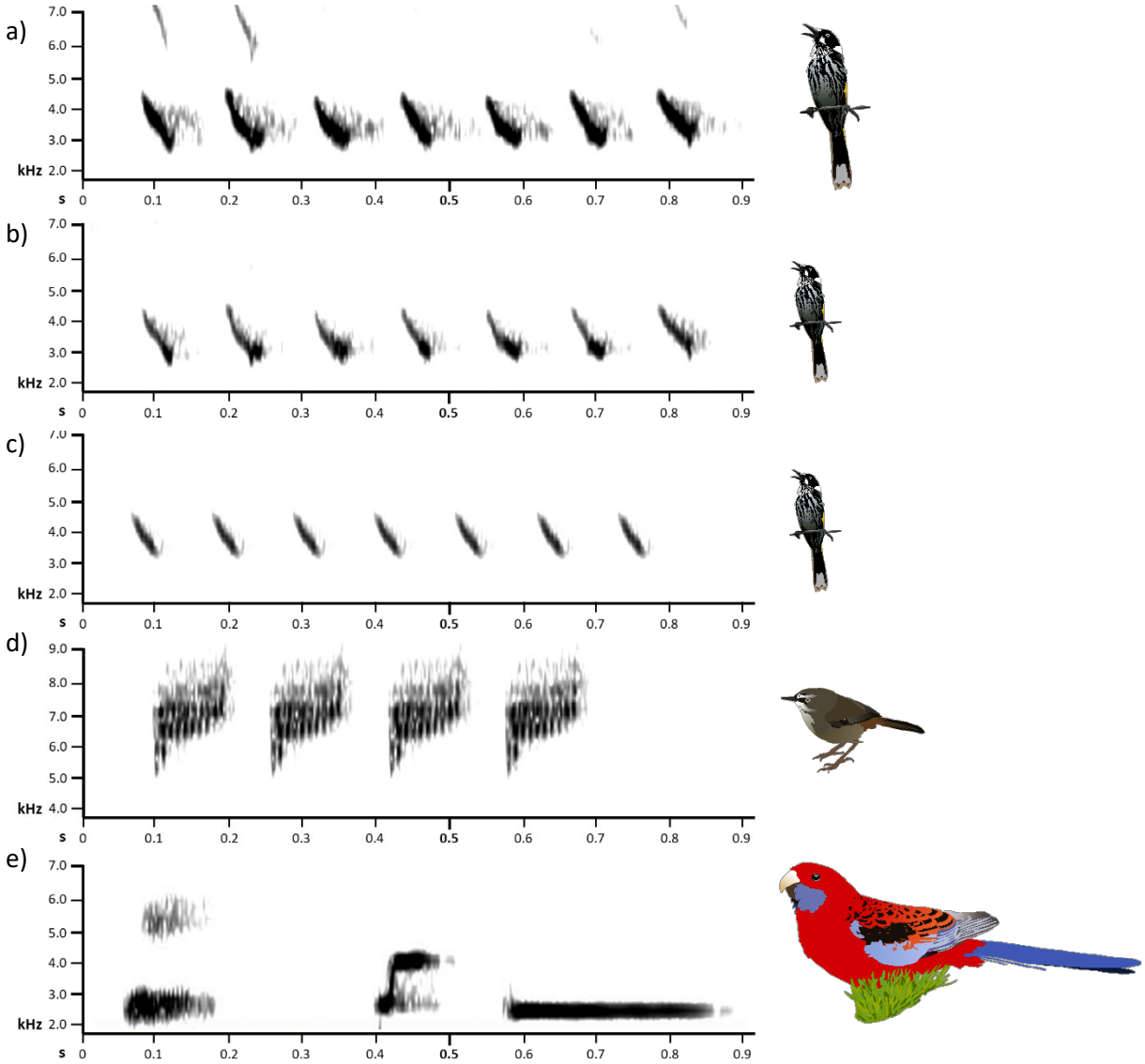


Figure 4.3. *Spectrograms showing examples of a) 7-element New Holland honeyeater alarm at natural amplitude, b) 7-element honeyeater alarm at reduced amplitude with degradation, c) 7-element honeyeater alarm at reduced amplitude without degradation, d) white-browed scrubwren alarm at natural amplitude, and e) crimson rosella contact call. Calls a) – c) were recorded from the same individual. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9ms with an overlap of 50% and a frequency grid resolution of 172Hz. Images were created in Adobe Photoshop CC, and are not to scale.*

Experiment 1: Effect of alarm call distance

Birds were presented with 3 playbacks: (1) a 7-element alarm call at natural amplitude of 70 dB at 6 m, (2) a degraded version of the same 7- element call at an amplitude of 57.5 dB at 6 m, and (3) a crimson rosella bell call at an amplitude of 70 dB at 6 m as a neutral control. I used 20 unique, natural 7-element honeyeater aerial alarm calls to create the playbacks and standardised the inter-element interval to 85 ms (mean ± SE: 84.40 ± 0.05 ms). Each bird received a unique set of playbacks, and all alarm calls within a set came from the same individual. To degrade the calls, they were played back and re-recorded through the undergrowth from a distance of 25 m. This should create the impression that the degraded, reduced amplitude calls were produced at a greater distance from the focal individual, perhaps rendering them less relevant (Murray & Magrath, 2015; Naguib & Wiley, 2001). Nearby alarm calls should indicate an immediate threat and prompt flight to cover, whereas distant alarm calls may result in information seeking behaviour, such as scanning. I predicted that birds would respond more strongly to: a) the playbacks when they were foraging, and b) the playbacks simulating a closer caller.

Experiment 2: Effect of alarm calling species

Birds were presented with 4 playbacks: (1) a 7-element New Holland honeyeater aerial alarm call at natural amplitude of 70 dB at 6 m, (2) the same 7-element honeyeater aerial alarm call at a reduced amplitude of 57.5 dB at 6 m, (3) a 4-element white-browed scrubwren aerial alarm call at natural amplitude of 57.5 dB at 6 m, and (3) a crimson rosella bell call at an amplitude of 70 dB at 6 m as a neutral control. I created 20 7-element New Holland honeyeater aerial alarm calls and 20 4-element white-browed scrubwren aerial alarm calls by repeatedly pasting single elements from natural calls with good signal-to-noise ratios. The honeyeater elements were extracted from natural 7-element alarm calls. White-browed scrubwren aerial alarm calls are acoustically distinct from New Holland alarm calls (Fig. 4.3) with a peak frequency of 7 kHz and a double band of frequency modulation, but they also encode urgency in the number of elements (Leavesley & Magrath, 2005; Magrath et al., 2007). Their alarm calls may not be perceived as perfectly relevant, and consequently

reliable, from the perspective of the New Holland honeyeaters, as around 20% of their alarms are given to non-predators (Magrath et al., 2009a). I predicted that birds would respond more strongly to: a) the playbacks when they were foraging, b) honeyeater alarms presented at their natural amplitude compared with honeyeater calls presented at a reduced amplitude, which could indicate a more distant caller, and c) honeyeater alarm calls compared to scrubwren alarm calls, which may be less reliable.

Statistical Analysis

All statistical analyses were carried out in R version 3.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Generalised linear mixed effects models (GLMMs) were constructed with binomial error distributions and logit link functions, using the glmer() function of the lme4 package (Bates et al., 2016). I constructed the linear mixed effects models (LMMs) with normal error distributions and identity link functions, using the lmer() function of the lme4 package (Bates et al., 2016). I carried out pair-wise comparisons using the glht() function of the multcomp package (Hothorn et al., 2008). In all cases, the full model with all terms of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance.

Model presentation experiment

Whether or not the birds detected the model, whether they fled and whether they gave alarm calls to the model were entered as the response variables in generalised linear mixed effects models. For all three models, the position and sex of the bird were entered as fixed effects, and the identity of the focal individual was included as a random effect. To look at the latency to see the model, I used a linear mixed effect model. The position of the bird, the sex of the bird, the presentation order and the specific predator model exemplar were entered as fixed effects, and the identity of individual birds was included as a random effect.

Playback experiments

As birds never fled to the controls, these were dropped from the analyses. The fleeing response was entered as the binary response variable in a generalised linear mixed effects model. The playback type, the position of the bird and the sex of the bird were entered as fixed effects. The identity of the individual bird was entered as a random effect. The latency to respond underwent a logarithmic transformation to improve fit before being entered as the response variable into a linear mixed effects model. The playback type, the position of the bird, the sex of the bird, the day and the playback order within the day were entered as fixed effects. The identity of the individual bird was entered as a random effect.

4.4 RESULTS

Model presentations

Whether the birds were perched or foraging had no effect on the probability of responding to the model, but foraging birds took about 220 ms longer to detect the model than perched birds (Table 4.1a, b, p 102; Fig. 4.4a, p 103), which supports the hypothesis that foraging birds have restricted personal information. The position of the bird did not affect the probability of giving an alarm call, but foraging birds were almost three times more likely to flee to cover than perched birds, which is consistent with the idea that they have less information and consequently overestimate risk (Table 4.1c, d; Fig. 4.4b). There were no sex differences in the probability of responding to the model or the latency to detect it; however, males were more likely to produce an alarm call than females (Table 4.1c; Fig. 4.4c).

Playback Experiment 1: Effect of alarm call distance

As predicted, honeyeaters responded more strongly to playbacks when they were foraging and when the social information was of higher quality. There was no significant interaction between playback type and the position of the focal bird (Table 4.2, p 105). The honeyeaters were more than twice as likely to flee into cover when they were foraging than when they were perched (Table 4.2a;

Fig. 4.5a, p 103). Birds fled to cover only half as often in response to the alarm playbacks that simulated a distant caller than to those that seemed closer (Table 4.2a; Fig. 4.5b). The sex of the bird did not affect the probability of fleeing (Table 4.2a). The latency to respond to the playbacks was not affected by the position or sex of the focal bird, but there was a weak trend indicating that birds responded more slowly to the more distant playbacks (Table 4.2b).

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) GLMM	**Probability of responding to model**						
		(Intercept)		1.06±1.03			
		Position (For)	Per	0.41±0.92	1	0.20	0.65
		Sex (Female)	Male	1.20±1.07	1	1.41	0.24
		Order (First)	Second	0.05±0.93	1	0.00	0.95
	Random term	*Bird - variance*		0.76			
(b) LMM	**Latency to see model**						
		(Intercept)		37.33±5.59			
		Position (For)	Per	-11.56±4.89	**1**	**5.22**	**0.02**
		Sex (Female)	Male	-8.20±5.43	1	2.33	0.13
		Order (First)	Second	-0.87±5.01	1	0.03	0.86
	Random term	*Bird - variance*		26.44			
(c) GLMM	**Probability of giving an alarm call**						
		(Intercept)		-1.79±0.94			
		Position (For)	Per	0.13±0.80	1	0.02	0.87
		Sex (Female)	Male	2.58±0.92	1	10.15	**0.001**
		Order (First)	Second	-1.06±0.84	1	1.68	0.20
	Random term	*Bird - variance*		0.00			
(d) GLMM	**Probability of fleeing to model**						
		(Intercept)		-0.90±0.79			
		Position (For)	Per	-1.54±0.76	**1**	**4.49**	**0.03**
		Sex (Female)	Male	0.17±0.74	1	0.05	0.82
		Order (First)	Second	1.57±0.80	**1**	**4.28**	**0.04**
	Random term	*Bird - variance*		0.00			

Table 4.1. *Model Presentations: Outcomes of generalised linear mixed effects models (GLMM) and linear mixed effects models (LMM) to investigate a) the effects of bird position on the probability of seeing the model predator, b) the effects of bird position on the latency to see the model predator, c) the effects of bird sex on the probability of giving an alarm call to the model predator, and d) the probability of fleeing to the model. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

Playback Experiment 2: Effect of alarm calling species

Consistent with the previous experiment, the position of the birds again affected their propensity to flee. There was no significant interaction between playback type and the position of the focal bird, nor did sex affect the probability of fleeing (Table 4.2, p 105). However, birds were more than twice as likely when foraging than when perched (Table 4.2c; Fig. 4.6a, p 104). Birds were slightly

slower to react to playbacks when perched, taking about 40 ms longer than when they were foraging (Table 4.2d; Fig. 4.6b).

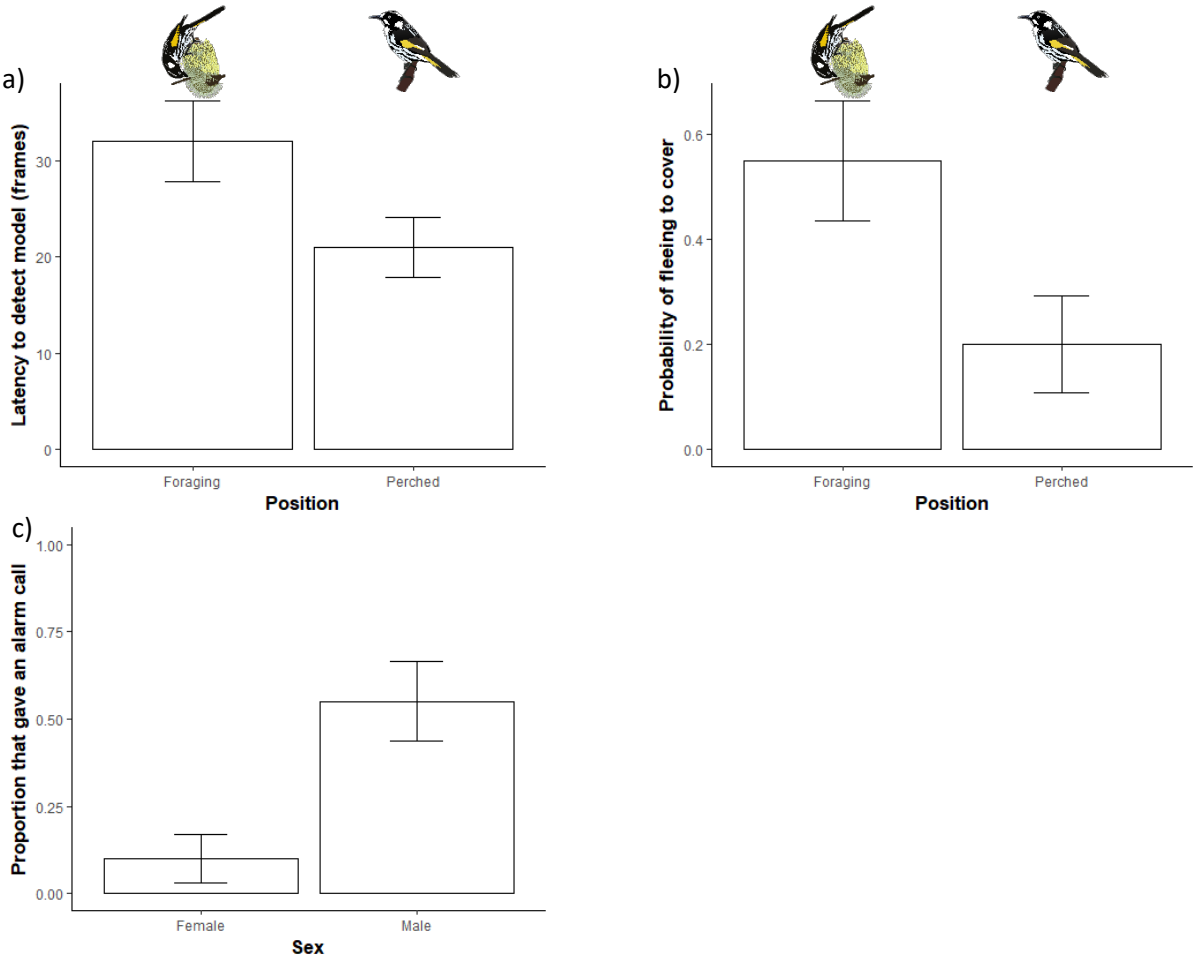


Figure 4.4. *Model presentations: a) The latency to detect the model predator in frames (1 frame = 20 ms), b) probability of fleeing to the model, and c) proportion of male vs female honeyeaters that gave an alarm call. Raw data shown. Columns represent means. Bars represent standard errors. N = 20 birds.*

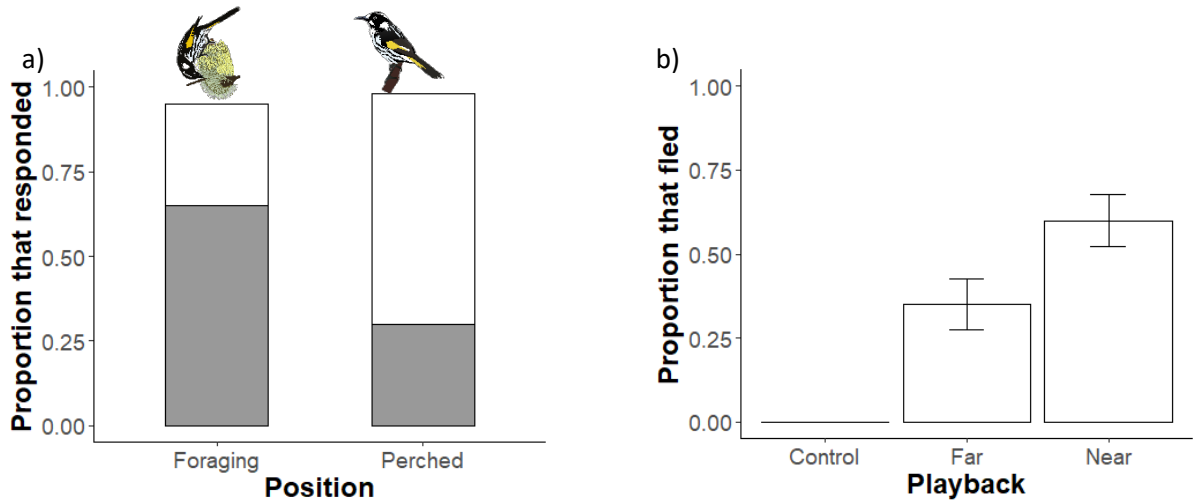


Figure 4.5. *Playback Experiment 1 – Effect of alarm call distance: a) Proportion of birds that responded in relation to their position. Dark columns represent immediate flees to cover. White columns represent other responses, including scans, scans followed by flees, and birds that landed outside of cover. No response not shown. b) Proportion of birds that fled immediately into cover to playbacks simulating different caller distances. Raw data shown. Columns represent means. Bars represent standard errors. N = 20 birds.*

Birds were more likely to flee, and responded faster, to conspecific than heterospecific alarms. As predicted, pairwise comparisons revealed that the birds fled more than twice as frequently to conspecific alarm calls at natural amplitude than to the scrubwren alarm calls (Tukey's test: z = -3.00, *p* = 0.008; Table 4.2c; Fig. 4.7a, p 106). The amplitude of the playbacks affected the probability of fleeing, as the honeyeaters were also more than twice as likely to flee to conspecific alarms at their natural amplitude than to the same calls at reduced amplitude (Tukey's test: z = -2.95, *p* = 0.009). However, the honeyeaters responded similarly quickly to honeyeater alarms played at their natural amplitude and at a reduced amplitude (Table 4.2d; Fig. 4.7b), which suggests that lower amplitude playbacks were not harder to detect. The identity of the calling species also affected the latency to respond: birds took around 100 ms longer to respond to the scrubwren alarms than to the honeyeater alarms at both natural (Tukey's test: z = 3.92, *p* = 0.0003) and reduced amplitude (Tukey's test: z = 4.01, *p* = 0.0002).

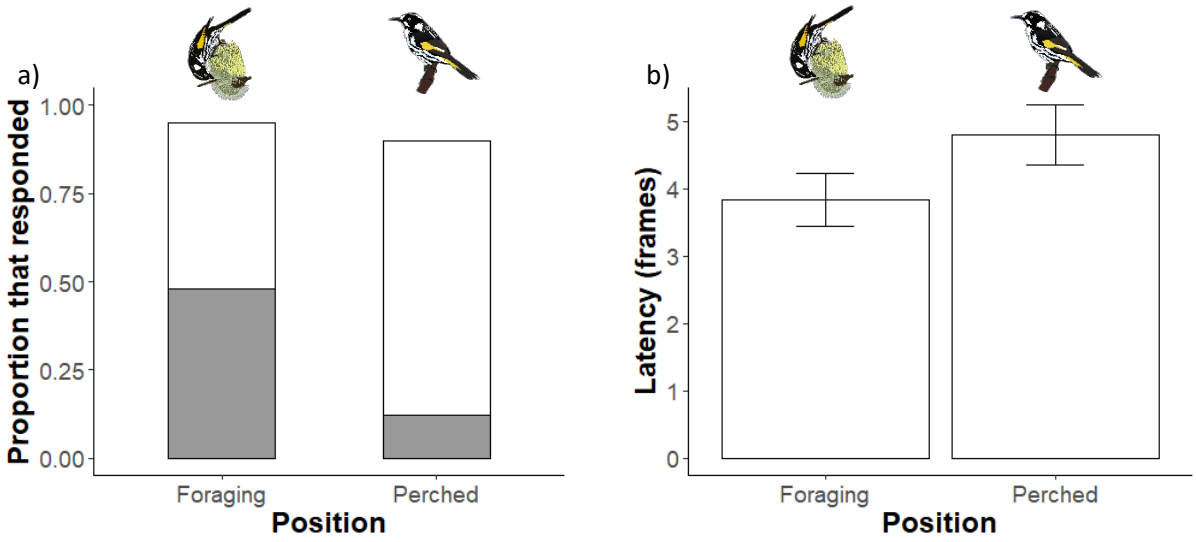


Figure 4.6. *Playback Experiment 2 – Effect of alarm calling species: a) Proportion of birds that responded to playbacks in relation to their position. Dark columns represent immediate flees to cover. White columns represent other responses, including scans, scans followed by flees and birds that landed outside of cover. No response not shown. b) Latency to respond to playbacks in frames (1 frame = 40 ms). Columns represent means. Bars represent standard errors. N = 20 birds.*

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Alarm call distance (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		2.32±1.13			
		Playback (Far)	Near	1.86±0.76	**1**	**8.18**	**0.004**
		Position (Foraging)	Perched	-2.54±0.82	**1**	**15.37**	**<0.0001**
		Sex (Female)	Male	-1.29±0.95	1	1.91	0.17
		Order (First)	Second	-2.17±0.94	**2**	**7.04**	**0.03**
			Third	-0.90±0.86			
		Day (One)	Two	-0.92±0.68	1	2.04	0.15
	Dropped terms	PB:Position (Far:Foraging)	Near:Perched	1.47±1.37	1	1.23	0.27
	Random term	*Bird - variance*		2.07			
(b) Alarm call distance (LMM)	**Latency to respond**						
		(Intercept)		1.32±0.20			
		Playback (Far)	Near	-0.24±0.13	1	3.63	0.056
		Position (Foraging)	Perched	0.09±0.13	1	0.57	0.45
		Sex (Female)	Male	0.04±0.19	1	0.04	0.84
		Order (First)	Second	-0.18±0.17	2	2.20	0.14
			Third	-0.18±0.18			
		Day (One)	Two	-0.19±0.13	1	1.43	0.49
	Dropped terms	PB:Position (Far:Foraging)	Perched:Male	-0.07±0.26	1	0.07	0.79
	Random term	*Bird - variance*		0.09			
(c) Alarm calling species (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		-0.35±0.69			
		Playback (NH-58dB)	NH-70dB	1.77±0.60	**2**	**13.51**	**0.001**
			SW-58dB	-0.05±0.62			
		Position (Foraging)	Perched	-2.31±0.55	**1**	**22.72**	**<0.0001**
		Sex (Female)	Male	-0.39±0.48	1	0.69	0.41
		Order (First)	Second	-0.30±0.66	3	0.50	0.92
			Third	-0.16±0.75			
			Fourth	-0.18±0.65]			
		Day (One)	Two	-0.33±0.49	1	0.46	0.50
	Dropped terms	PB:Position (NH-58dB:Foraging)	NH-70dB:Perched	0.17±1.36	2	0.07	0.99
			SW-58dB:Perched	0.20±1.62			
	Random term	*Bird - variance*		0.00			
(d) Alarm calling species (LMM)	**Latency to respond**						
		(Intercept)		0.83±0.19			
		Playback (NH-58dB)	NH-70dB	-0.01±0.15	**2**	**20.59**	**<0.0001**
			SW-58dB	0.60±0.15			
		Position (Foraging)	Perched	0.24±0.12	**1**	**3.96**	**0.047**
		Sex (Female)	Male	0.13±0.12	1	1.23	0.27
		Order (First)	Second	0.14±0.17	3	4.75	0.19
			Third	-0.22±0.19			
			Fourth	-0.08±0.18			
		Day (One)	Two	0.11±0.12	1	0.86	0.35
	Dropped terms	PB:Position (NH-58dB:Foraging)	NH-70dB:Perched	0.02±0.30	2	0.08	0.96
			SW-58dB:Perched	-0.06±0.31			
	Random term	*Bird - variance*		0.00			

Table 4.2. *Playback Experiments: Outcomes of generalised linear mixed effects models (GLMM) and linear mixed effects models (LMM) to investigate a) the effects of alarm call distance on the probability of fleeing to cover, b) the effects of alarm call distance on the latency to respond to playbacks, c) the effects of alarm calling species on the probability of fleeing to cover, d) the effects of alarm calling species on the latency to respond to playbacks. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

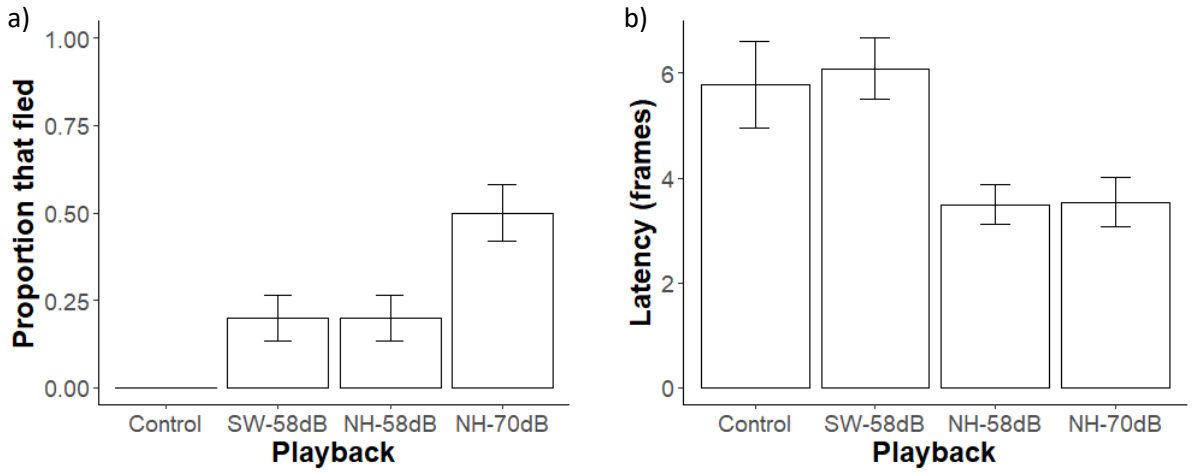


Figure 4.7. *Experiment 2 – Effect of alarm calling species: a) Proportion of birds that fled immediately to cover to playbacks from conspecifics and heterospecifics. b) Latency to respond to playbacks in frames (1 frame = 40 ms). SW-58dB = scrubwren alarm presented at 58 dB; NH-58dB = honeyeater alarm presented at 58 dB; NH-70dB = honeyeater alarm presented at 70 dB. Columns represent means. Bars represent standard errors. N = 20 birds.*

4.5 Discussion

Individuals with reduced personal information about danger were more reliant on the social information provided by con- and heterospecific alarm calls. Birds were more likely to flee to cover if the alarm playbacks were presented when they were foraging with a restricted view of their environments than when they were perched. This is consistent with the findings of the model presentation experiment, in which foraging birds took significantly longer to spot the predator. The quality of the social information also affected responsiveness, with heterospecific alarm calls and playbacks simulating a more distant caller prompting fewer individuals to flee. These results demonstrate that birds can use, and weigh, information from different sources in order to make flexible decisions in the context of danger.

Amount of personal information

The results of the model presentation experiment support the idea that perched birds have better access to personal information about danger than foraging birds. Individuals that were perched reacted on average 220 ms sooner to the model predator than foraging birds. This is about the time it takes for a honeyeater to initiate an immediate flee to an alarm call (Chapter 3) and a hunting raptor could gain up to 5 m in that time (Goslow, 1971; Hilton et al., 1999), making it a meaningful difference

in reaction time. However, it is likely to be an underestimate of the differences in detection between perched and foraging birds, as the models were always presented on the same side of the bush as the side on which the birds were feeding. In reality, predators could approach from the opposite side to a feeding bird, reducing the ease of detection and likely resulting in slower reaction times for feeding birds. Nonetheless, the greater delay to react in foraging birds is consistent with previous work that found that birds take longer to detect oncoming models when their heads are down (Devereux et al., 2006; Lima & Bednekoff, 1999; Tisdale & Fernández-Juricic, 2009). The reaction times recorded in this study were slightly slower than has been found in some other species, but the model was presented at a greater distance and did not travel towards the focal bird in this study (Cresswell et al., 2009; Fernández-Juricic et al., 2012; Kaby & Lind, 2003; van der Veen & Lindström, 2000).

Individuals could be expected to adopt a strategy of better-safe-than-sorry when presented with conflicting information about danger, as the costs of ignoring information could be very high. However, across all experiments, perched birds rarely fled to cover. As such, it seems that, when presented with model predators, individuals with a clearer view of the predator could more accurately assess the degree of danger they were in, while in the playback experiments birds that could see there was no predator nearby devalued the social information provided by alarm calls. The pattern of social information use found here across different feeding strategies in individual honeyeaters is consistent with research on species differences in reliance on heterospecific alarm calls, where studies have found that species that spend more time foraging low in the canopy tend to respond more strongly to alarm calls than species that hawk for insects from perches (Goodale et al., 2010; Martínez & Zenil, 2012; Ridley et al., 2014).

Perched honeyeaters did not ignore the alarm calls entirely. Birds that did not immediately flee engaged in other anti-predator behaviours, such as scanning or fleeing after a period of scanning. As perched birds can see further, they may therefore have enough time to gather further personal information before deciding whether to flee. Foraging birds may be targeted by predators more often than vigilant individuals (Krause & Godin, 1996; Roth et al., 2006; cf. Cresswell et al., 2003a), which

could explain why in one experiment birds responded more rapidly to playbacks when they were foraging. As a result of their greater vulnerability, foraging birds could be primed for danger and able to react more quickly. Together, these results suggest that birds integrate both sources of information, which enables them to reduce energetically expensive flights and to avoid potentially paying a fatal price.

Quality of social information

The quality of the social information also played an important role in determining its use. The honeyeaters responded more strongly to alarm calls that simulated a caller nearby than to calls that had been degraded and attenuated to represent a more distant caller. Individuals calling from further away may potentially be a less relevant source of information or could provide less urgent information, as the threat is also likely to be more distant, resulting in receivers seeking further information about the threat, rather than fleeing immediately into cover (Murray & Magrath, 2015). As the honeyeaters showed similarly reduced responsiveness to conspecific calls played back at a reduced amplitude without degradation, it is possible that birds use amplitude alone as a proxy for distance or that quieter calls signal lower urgency (Leger et al., 1979; Murray & Magrath, 2015; Naguib & Wiley, 2001).

Eavesdropping on heterospecific alarm calls can provide a valuable source of information, as it means there are more individuals looking out for danger, some of which may be better at detecting predators than others (Magrath et al., 2015a). However, honeyeaters were less likely to flee to heterospecific alarm calls than to conspecific calls when both were played at their natural amplitudes. Several studies have reported lower response rates to heterospecific alarm calls, likely because heterospecifics are not vulnerable to the same suite of predators, rendering some of their alarm calls irrelevant to eavesdroppers (Magrath et al., 2015a). In this chapter, I found that not only did birds flee less frequently to heterospecific alarm calls, the honeyeaters also responded more slowly to the scrubwren alarms. Weaker signals are associated with slower reaction times (Murray, 1970; Raab & Fehrer, 1962), but the quieter amplitude of the scrubwren alarms is not sufficient to explain the difference as the birds responded similarly swiftly to the New Holland calls played at both the natural

and reduced amplitude. It is possible that New Holland honeyeaters have to learn to recognise the acoustically dissimilar scrubwren alarm calls (Fallow et al., 2011; Haff & Magrath, 2012, 2013; Magrath et al., 2009b), which could lead to a longer processing time for the learnt calls (Boschen et al., 2015; Disterhoft et al., 1977). Previous work in birds has found some evidence that they are able to discriminate more quickly between conspecific calls than between heterospecific calls, and in humans, *Homo sapiens*, individuals react more slowly to words in their non-native language (Dooling et al., 1992; Izura & Ellis, 2002). Together, these results suggest that there can be both clear and subtle advantages to using conspecific information.

Sex differences

Consistent with the findings in Chapter 2, male New Holland honeyeaters were more likely to produce alarm calls when presented with a threat than females. As this experiment was carried out in late summer, it implies that male-biased alarm production is not an artefact of the spring breeding season but is consistent throughout the year. In this species, males appear to be the primary providers of information about danger.

Conclusion

In this chapter, I demonstrate that New Holland honeyeaters can make flexible decisions in the context of danger by differentially valuing information from distinct sources, using their own personal observations as well as information from others. These results support previous work showing that not all information on danger is equal – both the type of information (Cronin, 2013; Kendal et al., 2004; van der Veen, 2002) and its quality (Furrer & Manser, 2009; Magrath et al., 2009a; Rieucau & Giraldeau, 2009) can have significant effects on how it is weighed, even during very rapid flee responses. By incorporating information from multiple sources, birds can mitigate the costs of fleeing to false, or irrelevant, alarm calls while avoiding fatal predator encounters when they are most vulnerable.

Chapter 5

Honeyeaters value both the number and relevance of alarm callers when integrating social information from multiple sources

5.1 SUMMARY

Dangerous predators are often associated with a chorus of alarm calls from several individuals and species. Yet we understand relatively little about how individuals use information derived from multiple sources. Social information is not always accurate, resulting in false alarms and selecting for strategies to reduce the risk of responding to erroneous information. One way to minimise unnecessary responses is to adopt a simple quorum rule by only responding when the number of signals, or signalers, crosses a particular threshold. However, species differ in their vulnerability to predators and, consequently, the relevance of the information conveyed by their alarm calls from the perspective of heterospecific eavesdroppers may vary considerably. In such cases, simple rules based on the quantity of information may not result in the optimal response, and eavesdroppers may be selected to adjust their responses according to the relative reliability of the calling species instead. In this chapter, I used a combination of natural observations and playback experiments to New Holland honeyeaters to determine the value of social information from alarm calls produced by single and multiple sources, both within and across species. I found that, during natural predator encounters, more dangerous threats were associated with a larger number of alarm calls being produced by single individuals, a greater number of individuals giving alarm calls, and a greater number of species producing alarm calls. Honeyeaters, however, were no more likely to respond to playbacks of two conspecific alarm calls from one individual than to one call from the same bird, suggesting that multiple calls from a single caller are perceived as redundant by receivers. In contrast to this, they did respond more strongly to playbacks consisting of two conspecific callers rather than a single caller. The results of these two experiments indicate that honeyeaters only value additional information if it is derived from an independent source. When eavesdropping on the alarm calls of two unreliable species, which gave alarms that were not always relevant to honeyeaters, honeyeaters appeared to pay attention to the number of species calling. They were both more likely to flee and took longer to resume feeding when the two species called together than when either called alone. However, when one of the calling species was more reliable than the other, the order in which the two species called

determined whether or not the honeyeaters fled. Furthermore, the birds adjusted the weighting of the information according to its reliability and responded for an intermediate duration to the playbacks in which both species called. These findings demonstrate that birds are able to make sophisticated decisions about the degree of danger they face by attending to both the quantity and the relevance of information when listening to multiple alarm calls from conspecific and heterospecific callers.

5.2 INTRODUCTION

The sudden appearance of a hunting hawk is often accompanied by a chorus of alarm calls from the avian community upon which it preys (Gaddis, 1980; Goodale & Kotagama, 2005a, 2008b). Although this warning chorus contains a multitude of sounds from several individuals and species, acoustic playback experiments typically present a single stimulus from a single individual. As such, we know very little about how animals respond to multiple signals during a potentially fatal situation. In this chapter, I present New Holland honeyeaters, *Phylidonyris novaehollandiae*, with alarm calls from single conspecifics, multiple conspecifics or multiple species to determine how birds evaluate the quantity and the relevance of social information about danger in a community.

Social information of danger

Predation represents a significant selective force, and animals have evolved anti-predator strategies to improve predator detection and reduce the risk of being eaten (Caro, 2005). Vigilant behaviours, such as adopting a sentinel position or scanning, can enable individuals to detect predators directly, acquiring detailed personal information on the predator and its whereabouts (Cresswell et al., 2003b; McGowan & Woolfenden, 1989; Robinson, 1981; Whittingham et al., 2004). While personal information is likely to be accurate, it can be costly to gather because it can reduce opportunities to engage in other behaviours such as feeding (Giraldeau et al., 2002; Kendal et al., 2009). But many species produce alarm calls when they detect a threat, an anti-predator signal that warns others about danger (Caro, 2005). These warning calls are a form of social information that can be obtained indirectly from other individuals. They are a cheap source of information, as individuals can carry out non-vigilant activities and rely on others to detect danger for them (Hollén et al., 2008b).

The downside to depending on information provided by others is that it might not always be reliable (Searcy & Nowicki, 2005). Individuals may make mistakes in predator detection or they may use alarm calls deceptively to monopolise a resource, both of which will result in false alarms (Flower, 2011; Gyger et al., 1987; Haftorn, 2000; Møller, 1988; Munn, 1986; Sommer, 2011; Wheeler, 2009). Ignoring true alarms could be fatal but fleeing to false alarms can be energetically expensive or result

in lost resources (Butler, 1991; Flower, 2011; Møller, 1988; Nudds & Bryant, 2000). While the many-eyes hypothesis postulates that the probability of predator detection increases with an increasing number of individuals looking out for danger (Lima, 1995), the chance of false alarms occurring will also rise when there are more potential signalers present (Beauchamp, 2010). As such, individuals need to adopt strategies to mitigate the costs. One way to limit unnecessary escape flights would be to scan before fleeing, acquiring personal information to confirm the veracity of the call (Cresswell et al., 2009; Quinn & Cresswell, 2005). Individual recognition would also allow animals to selectively attend to calls given by individuals known to be reliable and to ignore unreliable alarm callers (Blumstein et al., 2004b; Cheney & Seyfarth, 1988; Hare & Atkins, 2001). Alternatively, animals could take advantage of the presence of multiple signalers, or signals, and use the number of signals to weight their confidence in the information (Cresswell et al., 2000; Robert, 1997).

The repetition of a signal by a single individual could convey additional information and impact the response of receivers. Signal repetition is a common way of enhancing the detection of that signal through redundancy (Price, 2013; Wiley, 2006). Calling repeatedly boosts the chances that receivers will hear the call, but it also confirms the message of the call and in doing so, increases the signal accuracy and the certainty of the receivers (Partan & Marler, 2005). Alternatively, calling more than once gives signalers the opportunity to update their message (Payne & Pagel, 1997). By adjusting the intensity of the signal, callers can communicate changes in their motivation. For example, European blackbirds, *Turdus merula*, increase the number of mobbing calls they produce in the seconds before they initiate flight (Andrew, 1961). Finally, repeated signals can also serve to enhance the message, resulting in a cumulative effect (Payne & Pagel, 1997). California ground squirrels, *Spermophilus beecheyi*, and great tits, *Parus major*, both respond for longer when presented with a greater number of calls from a single individual (Lind et al., 2005; Loughry & McDonough, 1988).

Information acquired from several independent sources is likely to be more reliable than information derived from a single source (Sumpter & Pratt, 2009). According to the signal redundancy hypothesis, signals with multiple components across different modalities have greater signal reliability

(Johnstone, 1996). The same argument could be applied at the level of signaler: while one individual may erroneously alarm call to a harmless species, even repeatedly, it is considerably less probable that two or three individuals will simultaneously make the same mistake. In Belding's ground squirrels, *Spermophilus beldingi*, multiple alarm calls from a single individual were a less reliable sign of danger than calls from multiple individuals (Robinson, 1981). This means that animals should attend not just to the number of signals, but also to how many individuals are signaling. Receivers can do this by adjusting the strength of their responses according to the number of callers. Sciurids show longer responses when presented with alarm calls from two callers, rather than one (Blumstein et al., 2004b; Sloan & Hare, 2008), primates use numerical assessment to adjust their behaviour in inter-group contests (van Belle & Scarry, 1998; Wilson et al., 2001), and ants are more likely to follow trails laid down by a larger number of individuals (Grüter et al., 2011). Animals could also adopt a simple quorum rule, requiring a certain number of individuals to signal first before investing in fleeing (Robert, 1997). The quorum can be flexibly adjusted according to the reliability of the social information or the number of individuals present, with more individuals resulting in a higher threshold (Kurvers et al., 2014; Robert, 1997; Romey & Kemak, 2018).

Eavesdropping on heterospecific alarms

Eavesdropping on the alarm calls of other species can both increase the number of eyes looking out for danger and the number of false alarm calls (Magrath et al., 2015a). Different foraging strategies and feeding heights can result in variation in species' abilities to spot danger, making it advantageous to pay attention to other species' calls (Goodale & Kotagama, 2005b). Birds that feed high in the canopy and hawk for insects or have sentinels looking out for danger are more likely to be attended to than ground feeders (Goodale & Kotagama, 2008b; Ridley et al., 2014). However, heterospecifics are unlikely to be vulnerable to precisely the same set of threats, which will render some of their alarm calls irrelevant to eavesdroppers. Species with a larger range of overlapping predators will consequently be perceived as more reliable than species that share few predators with the eavesdropper (Elvidge & Brown, 2015; Hua et al., 2016; Kitchen et al., 2010; MacLean & Bonter,

2013; Munoz et al., 2015). For example, superb fairy-wrens, *Malurus cyaneus*, and New Holland honeyeaters are both small passerines that share some predators, but fairy-wrens are smaller and are consequently more vulnerable to some threats than the honeyeaters (Magrath et al., 2009a). From the perspective of the fairy-wrens, honeyeater alarm calls are a reliable signal of danger and fairy-wrens usually fled to those calls. In contrast, fairy-wrens give a large number of alarm calls to threats that are irrelevant to the honeyeaters, and honeyeaters rarely fled to fairy-wren alarms. This asymmetry in response between species could therefore be related to signal reliability from each species' perspective (Magrath et al., 2009a).

Little is known about how individuals would respond if presented with multiple calls from more than one heterospecific species. A larger number of species calling could be a reliable indication that a predator is present, that the predator takes a broader range of prey, or that the predator is more dangerous. Thus, the number of signalers could convey certainty, relevance or risk. A study on the mobbing behaviour of European bird flocks found that more species mobbed in response to the more dangerous predator's call (Dutour et al., 2016). Furthermore, a similar number of species approached playbacks of the more dangerous predator's vocalisations and of a multi-species mobbing chorus, suggesting a multi-species chorus is a good indicator of predator presence. In either case, a greater number of calling species should prompt a stronger response from eavesdroppers. Eavesdropping individuals could therefore use simple quorum rules, based on the number of species signalling, to determine their reaction.

Given the variation in species' vulnerabilities, eavesdroppers could moderate their responses to multiple callers according to the relevance and accuracy of the specific species involved. If there is a large discrepancy in the relative reliability of the calling species, eavesdroppers may show an intermediate level of response to the combination, which falls between the responses given to the two species calling alone (Fraker, 2009). Alternatively, a difference in reliability may result in stimulus dominance, where eavesdroppers disregard the signals from the less reliable species and attend only to the more reliable caller, responding similarly to all choruses, mixed-species or not, in which that

species calls (Goodale & Kotagama, 2008b). Finally, the eavesdropper may respond more strongly to two species calling together than one calling alone if the region of overlap between the heterospecifics' two sets of predators coincides with the vulnerability of the eavesdropper (Magrath et al., 2015a). In support of stimulus enhancement, research using mimetic alarm calls found that a "mixed species" chorus prompted a stronger response than alarm calls derived from a single species (Igic et al., 2015), but this has not been investigated outside of a mimetic context.

Aims of the study

I tested how New Holland honeyeaters value social information on danger derived from single and multiple sources, both within and across species. First, I collected observational data during natural predator encounters to determine the contexts in which predators prompted multiple alarm calls and to assess whether multiple alarms and multiple calling species are more reliable signals of danger. I predicted that more dangerous threats would prompt both more individuals to give alarm calls and a greater number of species to call.

I followed the natural observations with a series of playback experiments on New Holland honeyeaters to test their responses to the number of conspecific calls and to the number of conspecific callers. As two alarm calls produced by the same individual do not represent independent sources of information, I did not expect more calls to receive a higher weighting than a single call. However, if honeyeaters use quorum rules when assessing multiple sources of social information, I predicted that they would respond more strongly to alarm calls given by two conspecifics than by a single caller. I also explored the mechanism by which honeyeaters discriminate between single and multiple conspecific callers.

Finally, I investigated the response of honeyeaters to alarm calls produced by two individuals from either two different heterospecific species or one species, where the reliability of the species presented varied. From the perspective of a honeyeater, a reliable species is one that gives alarm calls to the same stimuli that threaten the honyeaters themselves, whereas unreliable species also give alarm calls to stimuli that are not relevant to honeyeaters. New Holland honeyeaters are known to

differentiate between the alarm calls of reliable and unreliable heterospecifics when presented with single calls, making them a good species in which to test this (Magrath et al., 2009a). Again, I predicted that if quorum rules applied to heterospecific information as well, they would show stronger responses to calls from two species than to calls from a single species, but the effect of the number of species could be influenced by the relative reliabilities of the two calling species.

5.3 General Methods

Study site and species

Data were collected on a colour-banded population of around 70 New Holland honeyeaters between June 2014 and December 2017 in the Australian National Botanic Gardens in Canberra, Australia. These honeyeaters are small (20 g), pair-breeding passerines that feed primarily on nectar from flowering plants, as well as on arthropods. The botanic gardens comprise 40 ha of both natural vegetation and areas planted with Australian native flora. The birds in the study population were all resident in the gardens and accustomed to the presence of people.

New Holland honeyeaters give a distinct aerial alarm call to flying predators, which is composed of multiple elements of similar structure (Higgins et al., 2001; Jurisevic & Sanderson, 1994; Rooke & Knight, 1977) (Fig. 5.1a, p 122). Elements are considered to be part of the same call if they are separated by intervals of less than 200 ms and aerial alarm calls can contain between 1 and 100 elements, (personal observation). Urgency is encoded by incorporating more elements into alarm calls prompted by more dangerous threats (Chapter 3). Each element consists of a pure, descending whistle of approximately 33 ms in length. The elements are loud, with an amplitude of about 70 dB at 6 m (Magrath et al., 2009a), and relatively low in pitch (peak frequency mean: 3.6 kHz).

White-browed scrubwrens, *Sericornis frontalis*, and superb fairy-wrens are both small, insectivorous passerines that feed on the ground (scrubwren weight: 14 g; fairy-wren weight: 9-12 g) (Higgins et al., 2001; Higgins & Peter, 2002). They produce high-pitched, frequency-modulated alarm calls to aerial threats at an amplitude of around 58 dB at 6 m (scrubwren mean peak frequency: 7.1

kHz; fairy-wren mean peak frequency: 9.1 kHz; Fig. 5.1c, e) (Magrath et al., 2007, 2009a), and acoustically dissimilar contact calls (Fig, 5.1d, f). Like those of honeyeaters, these aerial alarm calls are composed of sequences of similar elements, and a greater number of elements is associated with greater danger (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). The honeyeaters appear to perceive scrubwren alarm calls as relatively reliable, whereas they respond infrequently to fairy-wren alarm calls, as fairy-wrens often call to non-predators (Magrath et al., 2009a).

Crimson rosellas, *Platycercus elegans*, are large (120-150 g), granivorous parrots that forage on the ground, in shrubs and in the canopy (Higgins, 1999). They seem to have a single, general alarm call, which is given when flushed (Higgins, 1999). The alarm calls are also composed of repeated elements, which may encode danger, but they are much longer and lower in frequency than the other species' (mean peak frequency ± SE: 2.95 Hz ± 0.16; mean duration ± SE: 141 ms ± 2.72) (Fig. 5.1g-h). The amplitude is intermediate between that of the honeyeaters and the wrens at approximately 65.5 dB at 6 m (mean amplitude ± SE: 65.58 dB ± 4.06). While rosellas are vulnerable to *Accipiter* hawks, they also alarm call to larger raptors such as wedge-tailed eagles*, Aquila audax*, which do not prey upon the smaller species (Marchant & Higgins, 1993; personal observation). Additionally, they appear to give a structurally similar call to both predators in flight and when mobbing perched raptors or ground predators (personal observation), which should result in their call being an unreliable signal of an aerial threat.

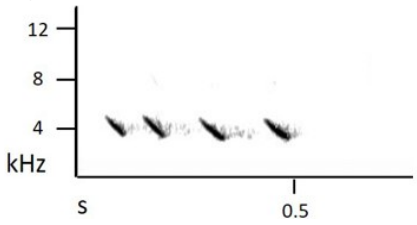
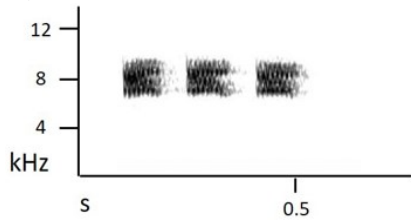
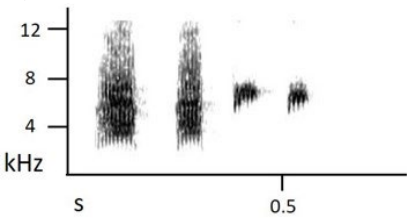
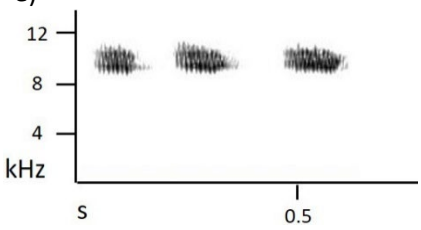
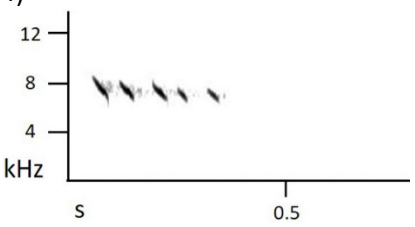
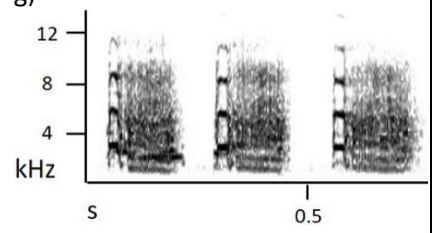
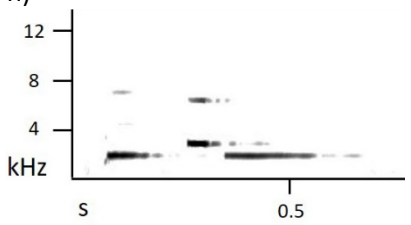
	Species	Alarm Call	Contact Call
RELIABLE	New Holland honeyeater (20g) 	a) 	b)
	White-browed scrubwren (14g) 	c) 	d) 
UNRELIABLE	Superb fairy-wren (11g) 	e) 	f) 
	Crimson rosella (120g) 	g) 	h) 

Figure 5.1. *Spectrograms showing examples of the playbacks presented throughout this chapter: a) 4-element honeyeater alarm, b) no honeyeater contact call was used as it could simulate an intrusion, rather than prompting a neutral response, c) 3-element white-browed scrubwren alarm call, d) white-browed scrubwren contact call, e) 3-element superb fairy-wren alarm call, f) superb fairy-wren contact call, g) 3-element crimson rosella alarm call, and h) crimson rosella contact call. Spectrograms were produced in Raven 1.5 using a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz. Species weight shown in parentheses. Drawings are not to scale.*

Statistical analyses

All statistical analyses were carried out in R version 3.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Linear models and general linear models were carried out using the lm() and glm() functions, respectively. Generalised linear mixed effects models (GLMMs) were constructed with binomial error distributions and logit link functions, using the glmer() function of the lme4 package (Bates et al., 2016). I constructed the linear mixed effects models (LMMs) with normal error distributions and identity link functions, using the lmer() function of the lme4 package (Bates et al., 2016). I carried out pair-wise comparisons using the glht() function of the multcomp package (Hothorn et al., 2008). In all cases, the full model with all terms of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance. Non-significant interactions were removed from the models, but all other terms remained.

5.4 NATURAL OBSERVATIONS

Methods

Recordings of natural alarm calls were made between 2014 and 2017 using a Marantz PMD70 and PMD661 Mk II solid-state digital recorders with a sampling rate of 44.1 kHz and 16 bits, and a Sennheiser ME66 shotgun microphone. The microphone was attached to my shoulder and I recorded continuously while the honeyeaters were followed at a distance of 10 – 20 m, allowing me to record alarm calls given during natural threat encounters observed in over 1500 hours in the field. While it was not always possible to identify the calling individuals, recordings were made in all honeyeater feeding areas around the gardens, reducing the degree of pseudoreplication.

The three most commonly observed flying prompts were red wattlebirds (*Anthochaera carunculata*, n=86 prompts), pied currawongs (*Strepera graculina*, n=108 prompts) and collared sparrowhawks (*Accipiter cirrhocephalus*, n=55 prompts). Wattlebirds are abundant in the gardens, and there are about 15 pairs of currawongs (L. Ascah, personal communication) and 2 pairs of *Accipiter*

hawks that breed in the botanic gardens each year. These three species represent an increasing threat level, so they were used to look at how the number of calls and callers varies with danger: wattlebirds are aggressive but non-predatory nectivores that can displace New Holland honeyeaters during competitive interactions over food; currawongs are primarily nest predators but will opportunistically target small birds; and sparrowhawks pose the greatest threat, as they principally feed on small birds around the size of New Holland honeyeaters (Higgins et al., 2001, 2006; Marchant & Higgins, 1993).

I generated spectrograms of the alarm call recordings using Raven Pro 1.4, a Hann window function with a 256 sample size, a temporal grid resolution of 2.9 ms with an overlap of 50% and a frequency grid resolution of 172 Hz. The spectrograms were then used to count the number of calls, callers and species associated with each prompt.

To ascertain the relative reliability of multiple alarm calls by single conspecifics, I looked at alarm recordings of natural encounters with threats in which only a single New Holland honeyeater called (N=96 prompts), and counted the number of alarm calls given by a single honeyeater.

I examined the recordings of natural encounters with threats in which only New Holland honeyeaters called (N=126 prompts), and counted the number of honeyeaters that alarm called to determine the relative reliability of multiple conspecific callers.

Finally, to determine the relative reliability of multiple heterospecific species calling, I looked at alarm recordings of all natural encounters with the three types of threat (N=209 prompts) and counted the number of species that gave alarm calls. I also recorded whether honeyeaters (109 choruses), scrubwrens (48 choruses), fairy-wrens (29 choruses) and rosellas (39 choruses) were the first to call when they participated in mixed-species alarm choruses that included both the focal species and at least one other species.

Statistical analyses

During natural observations, it was not always possible to identify the exact number of individuals calling to a prompt, so I converted all the counts into a binomial scoring system where 0 represented a single call, caller or species and 1 represented more than one call, caller or species.

I used generalised linear models to look at how the type of threat affects the probability of more than one alarm call being given by a single honeyeater, the probability that more than one honeyeater would give an alarm call and the probability that more than one species would produce an alarm call. In all three models, the type of threat was entered as a fixed effect. Pairwise comparisons were carried out to determine where the differences lay between the threats.

To look at the order in which the species called, I scored calling first as 1 and calling later as 0. This binary classification of order was entered into a generalised linear model as the response term, while the identity of the species was included as a fixed effect. Pairwise comparisons were carried out to determine where the differences lay between the calling species.

Results

More dangerous threats were more likely to prompt more than one alarm call from individual New Holland honeyeaters (Table 5.1a, p 127; Fig. 5.2a, p 126). Pairwise comparisons revealed that individual honeyeaters were three times more likely to produce multiple calls to sparrowhawks than to wattlebirds (Tukey's test: $z = -2.36$, $p = 0.04$).

Multiple honeyeaters were more likely to call to more dangerous prompts (Table 5.1b; Fig. 5.2b). More honeyeaters called to sparrowhawks than to wattlebirds (Tukey's test: $z = -4.28$, $p < 0.001$) or currawongs (Tukey's test: $z = 2.81$, $p = 0.014$).

Multiple species were more likely to call when faced with a more dangerous prompt (Table 5.1c; Fig. 5.2c). Sparrowhawks prompted more species to give alarm calls than wattlebirds (Tukey's test: $z = -6.40$, $p < 0.001$) or currawongs (Tukey's test: $z = 3.22$, $p = 0.004$), and currawongs prompted more species to call than wattlebirds (Tukey's test: $z = -4.51$, $p < 0.001$).

In the mixed-species alarm choruses in which they participated, New Holland honeyeaters were more likely to be the first species to give an alarm call than crimson rosellas (Tukey's test: z = 3.93, $p < 0.001$) and superb fairy-wrens (Tukey's test: z = 3.47, $p = 0.003$), whereas white-browed scrubwrens did not differ significantly from the other species (Tukey's test: all p > 0.05) (Table 5.1d; Fig. 5.2d).

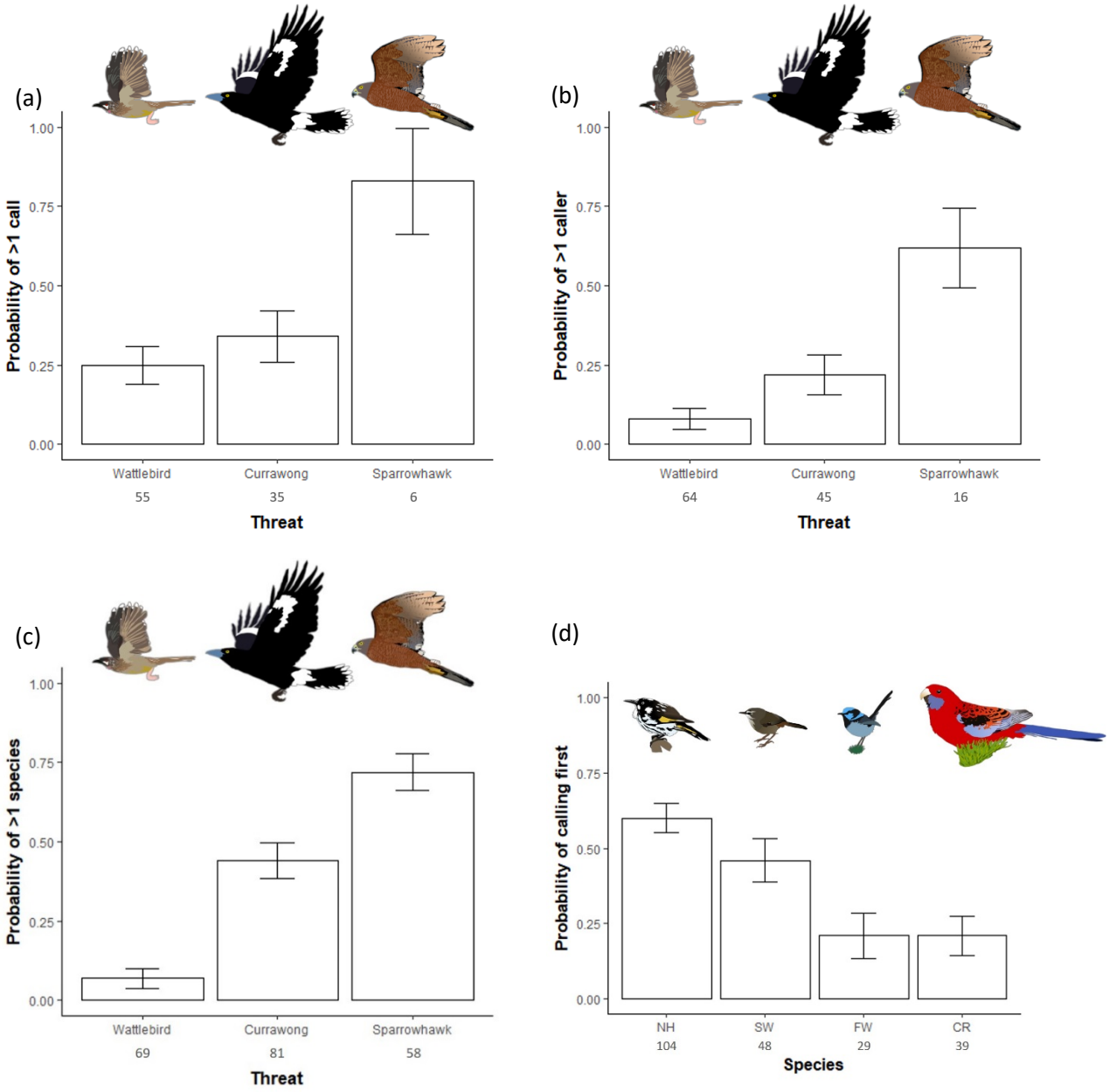


Figure 5.2. *Natural Observations: a) The probability that an individual honeyeater gave more than one alarm call to each threat, b) the probability that more than one honeyeater gave an alarm call to each threat, c) The probability that more than one species gave an alarm call to each threat, and d) the probability of each species being the first to call in mixed species choruses in which that species and at least one other species called to the same prompt. Columns represent means. Bars represent standard errors. Sample sizes indicated below columns. Species sizes are only roughly to scale within each figure.*

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Number of Calls (GLM)	**Probability of prompting >1 call**						
		(Intercept)		-0.69±0.24			
		Threat (CW)	SPH	1.46±0.41	**1**	**16.95**	**0.0003**
			WB	0.02±0.38			
(b) Number of Callers (GLM)	**Probability of prompting >1 caller**						
		(Intercept)		-1.57±0.29			
		Threat (CW)	SPH	2.13±0.40	**1**	**55.93**	**<0.0001**
			WB	-0.98±0.55			
(c) Number of Species (GLM)	**Probability of prompting >1 species**						
		(Intercept)		-0.22±0.22			
		Threat (CW)	SPH	1.19±0.37	**1**	**64.32**	**<0.0001**
			WB	-2.33±0.52			
(d) Order of Species (GLM)	**Probability of calling first**						
		(Intercept)		-1.35±0.40			
		Species (CR)	FW	0.01±0.61	**1**	**26.7**	**<0.0001**
			NH	1.74±0.44			
			SW	1.19±0.49			

Table 5.1. *Natural Observations: Outcomes of generalised linear models (GLM) to investigate a) the effects of threat type on the number of calls prompted by individual honeyeaters, b) the effects of threat type on the number of honeyeaters that called, c) the effects of threat type on the number of species that called, and d) the order in which species called during mixed-species alarm choruses. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

5.5 PLAYBACK EXPERIMENTS

General methods

The results of the natural observations suggest that the number of conspecific alarm calls, the number of conspecific callers, and the number of species calling are all reliable indications of the degree of danger. To test whether receivers use this information, I conducted four playback experiments on colour-banded honeyeaters between November 2016 and July 2017 in which I manipulated the number of conspecific calls and callers as well as the number of heterospecific species. All playbacks were prepared in Raven Pro 1.4. Playbacks were transferred as wave files to a Roland R-09HR and were broadcast via a custom-made amplifier and one or two Peerless speakers. One speaker was attached to my waist, giving an approximate height of 1 m; for experiments with two speakers, the second speaker was placed on a tripod and raised to a height of around 1 m. The birds' responses were recorded on the Panasonic HC-V770M camcorder filming at 50 frames per second at 1920x1080p, which was supported by Wizmount CU2pack over my shoulder.

Within each experiment, 12 unique playback sets were presented to the honeyeaters, and each bird received all playbacks within a set. Playback order was randomised within a blocked design

to minimise order effects. Birds were presented with the sounds when foraging. Playbacks were carried out a minimum of 30 minutes apart and there was a gap of at least 5 minutes following a natural alarm call. Playbacks were presented from a distance of 7 – 10 m. A total of 47 birds was used across the four experiments.

The video recordings of the responses were subsequently analysed frame-by-frame using Adobe Premier Pro and QuickTime. After recording the frame number of the playback onset, the soundtrack was removed to enable blind scoring. The response of the bird was scored as either a flee to cover during the playback (1) or not (0). The video analysis also allowed me to record the duration of the response, which was measured as the time from the onset of the response to the time when the birds resumed foraging or departed the feeding area. To account for the differences in playback lengths, the duration of the playback was subtracted from the duration of the response. This resulted in negative response durations if birds resumed foraging before the end of the playback. In the heterospecific experiments, I also recorded the latency to respond, which was measured as the time from the onset of the playback to the time when the birds initiated a response, generally starting with a rapid head movement or raising of the wings.

Statistical analyses

For each of the playback experiments, two models were created to test the effects of the playbacks on the fleeing responses and the duration of response. Generalised linear mixed effect models (GLMMs) were constructed to examine fleeing responses in each experiment. All GLMMs included sex of the focal bird as a fixed effect, and the identity of the focal bird as a random effect. For all experiments, the duration of response underwent a logarithmic transformation to improve fit before being entered as the response variable into a linear mixed effects model (LMM). The sex of the bird and the playback order were entered as fixed effects, and the identity of the individual bird and the specific playback set were entered as random effects.

In the playback experiments, birds showed little response to the control playbacks (see each experiment for details): they never fled to the controls, and they generally responded with a brief

glance or showed no reaction. As such, the controls were not included in the statistical analyses of the playback experiments. The inclusion of the playback order in the generalised linear mixed effects models usually caused the models to fail to converge, so it was excluded from the models in these instances.

5.6 PLAYBACKS OF CONSPECIFIC CALLS

a) Number of calls by the same individual

Methods

To determine the effect of the number of calls on conspecific receivers, I tested the response of 16 adult New Holland honeyeaters (8 male, 8 female) to playbacks. Each playback set consisted of 4 treatments (Fig. 5.3, p 130): 1) one honeyeater alarm call, 2) two honeyeater alarm calls, 3) one crimson rosella contact call, and 4) two crimson rosella contact calls as neutral controls. All alarm playbacks within a set were recorded from the same individual and consisted of natural 4-element calls. Crimson rosella contact calls were chosen as a neutral control, as they do not prompt fleeing and are generally ignored by honeyeaters (Magrath et al., 2009a). Playbacks were calibrated to 70 dB at 6 m, which is within the natural range for both calls. In the treatments that included two calls, the calls were separated by 2 s of silence.

Statistical analyses

The number of calls was included as a fixed effect in the statistical models that looked at the whether or not birds fled to cover and the duration of response.

Results

Despite the pattern of calling during natural observations, the number of alarm calls did not affect responsiveness (Table 5.2a, b, p 130). Birds were no more likely to flee to two alarm calls than to one call (Table 5.2a), nor did they take significantly longer to resume feeding after two alarm calls than after one (Table 5.2b).

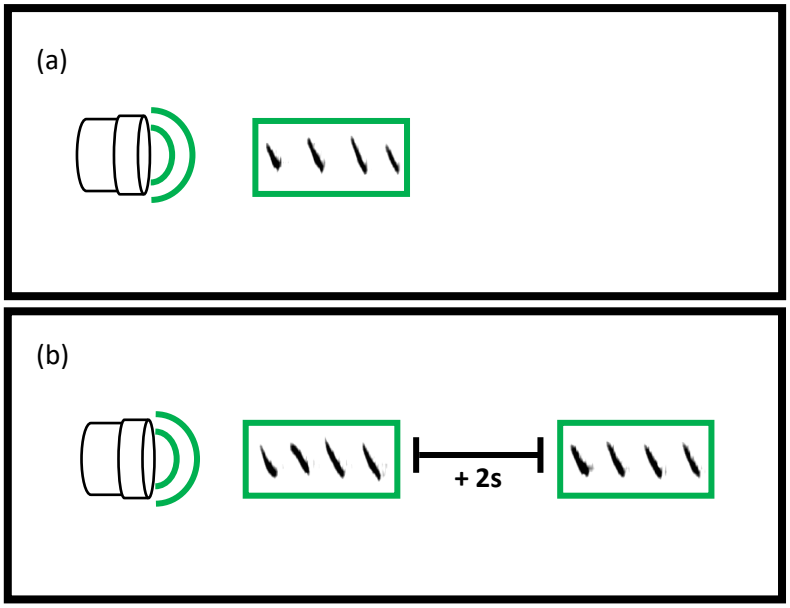


Figure 5.3. *Number of Calls by an Individual: Experimental design. Feeding birds were presented with either a) one or b) two calls from the same individual separated by 2s of silence.*

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Number of calls (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		2.54±2.48			
		Number (One)	Two	-0.61±1.13	1	0.30	0.58
		Sex (Female)	Male	-2.24±2.78	1	1.02	0.31
	Random term	*Bird - variance*		10.67			
(b) Number of calls (LMM)	**Duration of response**						
		(Intercept)		5.31±0.65			
		Number (One)	Two	0.262±0.37	1	3.32	0.069
		Sex (Female)	Male	0.09±0.63	1	0.02	0.88
		Order (First)	Second	017±0.52	3	1.34	0.72
			Third	-0.25±0.59			
			Fourth	0.32±0.62			
	Random term	*Bird - variance*		1.21			
		Playback set - variance		0.00			

Table 5.2*. Calling by conspecifics: Number of calls by the same individual. Outcomes of models to investigate: a) the effects of the number of conspecific calls by a single individual on the probability of fleeing to cover, and b) the effects of the number of conspecific calls by a single individual on the duration of response. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

b) Number of conspecifics calling

Methods

To look at the effect of the number of callers, I presented 24 adult New Holland honeyeaters (12 male, 12 female) with 4 treatments (Fig. 5.4, p 132): T1) two honeyeater alarm calls produced by the same individual and played from a single speaker with a 2 s silent interval, T2) two honeyeater alarm calls produced by the same individual and each played from separate speakers with a 2 s silent interval, T3) two honeyeater alarm calls, each produced by a different individual and each played from separate speakers with a 2 s silent interval, and T4) two honeyeater alarm calls produced by the two different individuals and each played from separate speakers but now with the two calls overlapping. The speakers were set up 5 m apart to simulate birds calling from different locations. All alarm calls consisted of natural 4-element calls and were calibrated to 70 dB at 6 m. In playbacks with overlapping calls, the second call began after the third element of the first call.

If honeyeaters use location as a proxy for number of callers, they should respond more strongly to playbacks using 2 speakers than to the single speaker treatment. If honeyeaters show vocal recognition of individuals, they should respond more strongly to the treatment with two callers from two locations than to a single caller presented from two locations. If honeyeaters use temporal overlap to identify multiple callers, they should respond more strongly to the treatment with overlapping calls than to the playbacks with a 2s gap.

Statistical analyses

The specific playback treatment was included as a fixed effect in the statistical models for both the flee response and the duration of response in this experiment. Planned comparisons were carried out to determine the effect of caller location, vocal recognition and the temporal overlap of calls, and to compare the clearest examples of one versus two callers.

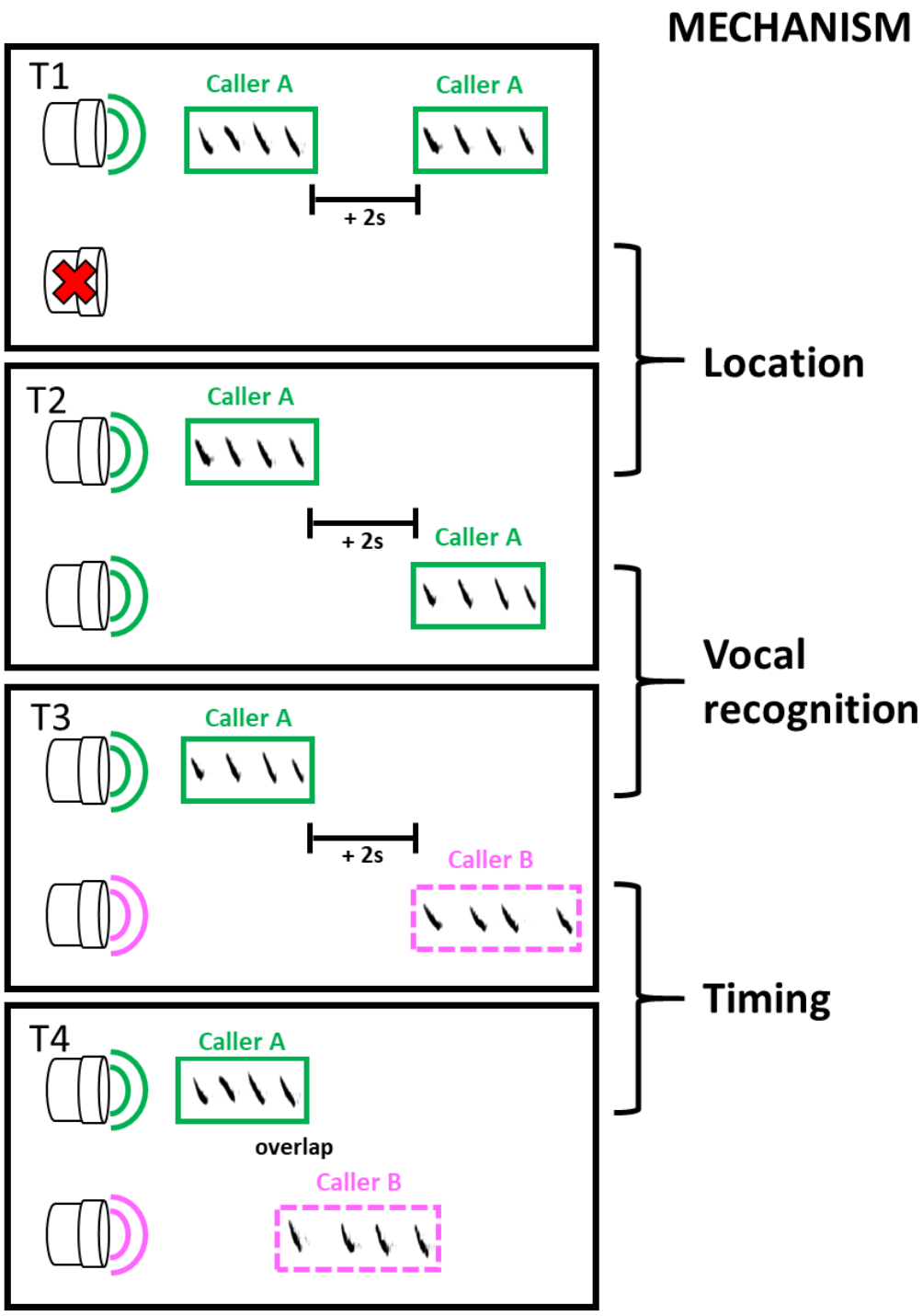


Figure 5.4. *Number of conspecific callers: Experimental design. Birds were presented with two alarm calls from either one (T1) or two (T2-T4) speakers. The alarm calls came from either one (T1-T2) or two (T3-T4) individuals and the calls were presented either consecutively with a 2 s gap (T1-T3) or overlapping (T4). Planned contrasts between treatments allowed me to look at whether birds pay attention to the number of callers in general using the two clearest examples of one and two callers (T1 vs T4) as well as to look at the possible mechanisms by which birds might determine the number of callers: location (T1 vs T2), vocal recognition (T2 vs T3) or timing (T3 vs T4).*

Results

Consistent with the results found in the natural observations, playbacks simulating two alarm callers prompted more birds to flee and resulted in longer responses than playbacks from a single individual (Table 5.3a, b, p 134; Fig. 5.5a, b, p 135). Birds fled about 30% more often to the playbacks simulating two callers calling from two locations with overlapping calls (T4) than to a single caller calling from one location with consecutive calls (T1) (Tukey's test: $z = 2.32$, $p = 0.02$), with the former treatment including all potential cues associated with the number of callers. However, when considering these three cues separately, pairwise comparisons revealed that the location of the speakers (Tukey's test: $z = 0.80$, $p = 0.42$), vocal recognition (Tukey's test: $z = -0.90$, $p = 0.37$), and whether the calls were presented consecutively or overlapping (Tukey's test: $z = 1.28$, $p = 0.20$) did not individually significantly affect the probability of fleeing.

Female honeyeaters fled to cover more often than males, fleeing about 75% of the time, whereas males only fled around 50% of the time (Table 5.3a; Fig. 5.5c).

Birds took almost three times as long to resume feeding following the treatment unambiguously simulating two callers (T4) compared to the treatment simulating a single caller from a single location (T1) (Tukey's test: $z = 4.14$, $p < 0.001$). But it was not clear to which cue the birds attended, as the duration of response was also not significantly affected by the location of the speakers (Tukey's test: $z = 0.38$, $p = 0.70$), vocal recognition (Tukey's test: $z = -1.64$, $p = 0.10$), or whether the calls were presented consecutively or overlapping (Tukey's test: $z = 1.36$, $p = 0.17$). On 5 occasions, playbacks prompted alarm calling by the focal individual. The playbacks consisted of two callers on 4 of the 5 occasions, and 3 of the 4 birds that called were female.

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Number of callers (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		3.85±1.66			
		PB (1 Caller;1 Location)	1 Caller; 2 Locations	0.86±1.06	**3**	**9.47**	**0.024**
			2 Callers; Consecutive	1.81±1.20			
			2 Callers; Overlap	3.18±1.37			
		Sex (Female)	Male	-3.06±1.66	**1**	**4.60**	**0.032**
		Order (First)	Second	-1.07±1.09	**3**	**22.09**	**<0.0001**
			Third	-3.89±1.50			
			Fourth	-4.38±1.50			
	Random term	*Bird - variance*		7.77			
(b) Number of callers (LMM)	**Duration of response**						
		(Intercept)		6.91±0.32			
		PB (1 Caller;1 Location)	1 Caller; 2 Locations	0.09±0.24	**3**	**14.52**	**0.002**
			2 Callers; Consecutive	0.49±0.24			
			2 Callers; Overlap	0.82±0.24			
		Sex (Female)	Male	-0.34±0.35	1	0.98	0.32
		Order (First)	Second	-0.39±0.24	**3**	**11.32**	**0.01**
			Third	-0.56±0.24			
			Fourth	-0.78±0.24			
	Random term	*Bird - variance*		0.57			
		Playback set - variance		0.00			

***Table 5.3**. Calling by Conspecifics: Outcomes of models to investigate a) the effects of the number of conspecific callers on the probability of fleeing to cover, and b) the effects of the number of conspecific callers on the duration of response. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

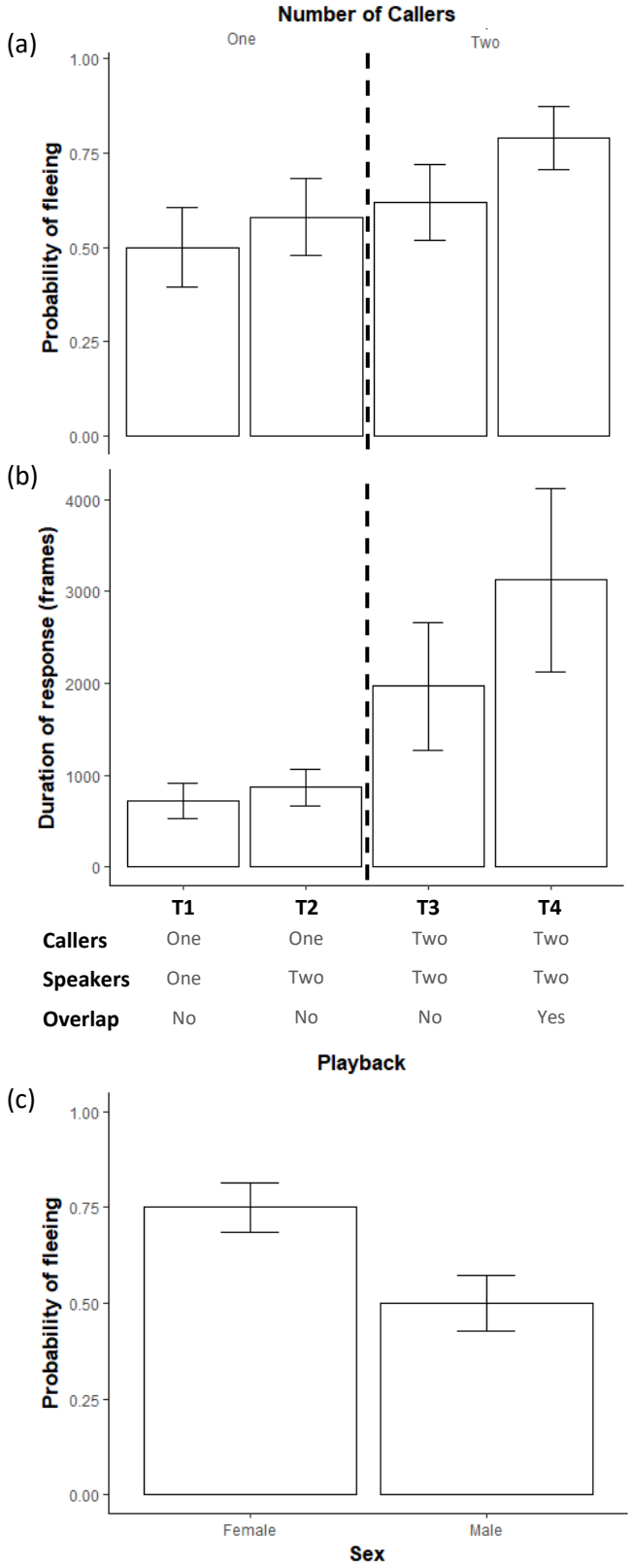


Figure 5.5. *Number of Conspecifics Calling Playback Experiment: a) Probability of fleeing to cover in relation to playback treatments, b) the duration of response in relation to playback treatments, and c) probability of fleeing to cover in relation to the sex of the focal bird. 1 frame = 20 ms. Columns represent means. Bars represent standard errors. N = 24 honeyeaters: 12 males, 12 females.*

5.7 PLAYBACKS OF HETEROSPECIFIC CALLS

General methods

To test the response of honeyeaters to alarm calls given by multiple species, I carried out two experiments on 24 adult New Holland honeyeaters (12 male, 12 female). As the natural observations of predator encounters suggested that multi-species choruses are a reliable sign of danger and that individual species differ in their propensity to call first, both experiments followed the same blocked design to test for the effect of the number of species while controlling for the order in which the participating species called during the multi-species treatments (Fig. 5.6, p 137). However, the specific species presented differed between experiments. The presentations were carried out over 2 days with 3 playbacks per day and no more than 2 alarm treatments were presented on a single day. The speakers were set up 5 m apart to simulate birds calling from different locations.

a) Heterospecific Playback Experiment 1: one species is more reliable than the other

Methods

In the first experiment, I presented calls from a reliable species, the white-browed scrubwren, and from an unreliable species, the crimson rosella. All presentations involved overlapping calls. There were 4 alarm treatments (Fig. 5.6): 1) two scrubwren alarm calls, 2) two crimson rosella alarm calls, 3) one scrubwren alarm call followed by one rosella alarm call, and 4) one crimson rosella alarm call followed by one scrubwren alarm call. Birds also received 2 of the following 4 control treatments (Fig. 5.6): 1) two scrubwren contact calls, 2) two crimson rosella contact calls, 3) one scrubwren contact call followed by one rosella alarm call, and 4) one crimson rosella alarm call followed by one scrubwren contact call. The number of individuals calling was kept constant across all playback treatments, with each playback containing calls from two different individuals. All birds received 6 playbacks in total, each receiving one single species control playback (1 or 2) and one mixed species control playback (3 or 4), in addition to all four alarm treatments. Birds were not presented with all possible controls in order to reduce the number of presentations done to a single individual. Calls were presented at the

natural amplitudes of the calling species, such that all scrubwren calls were calibrated to 57.5 dB at 6 m and all rosella calls were calibrated to 65.5 dB at 6 m.

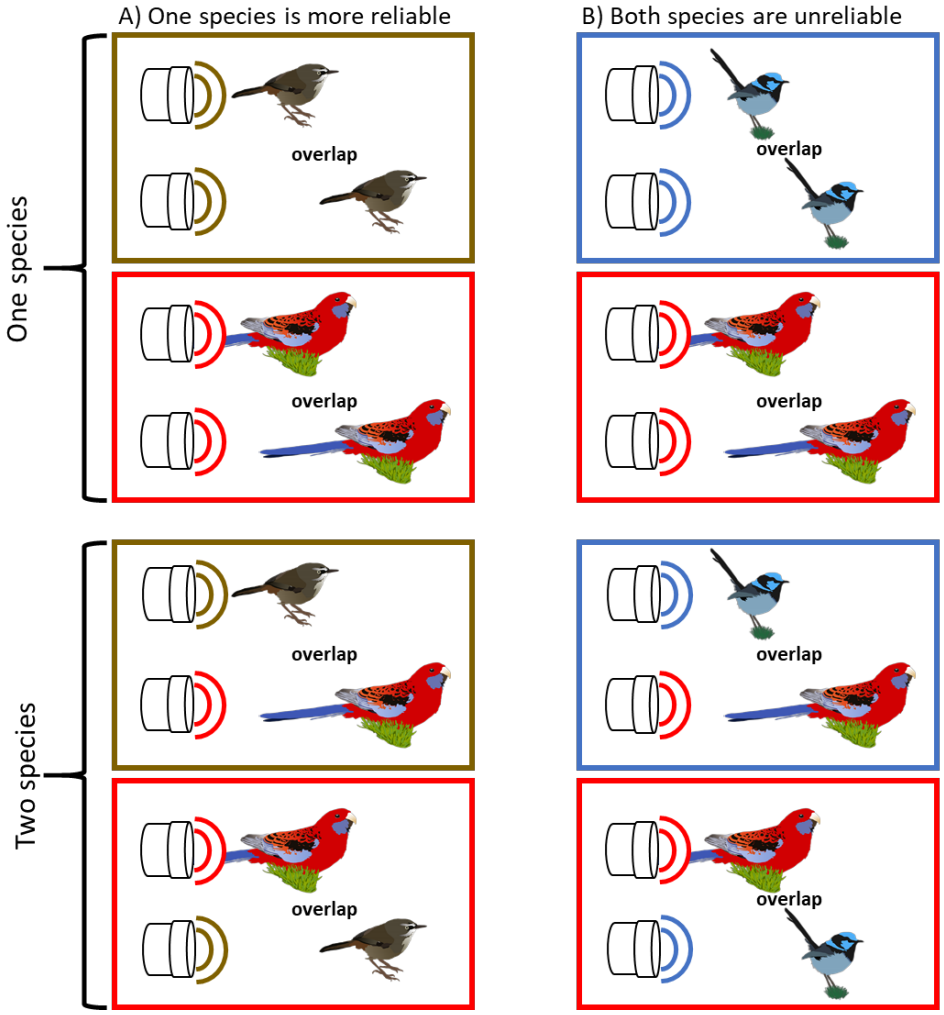


Figure 5.6. *Calling by heterospecifics: Experimental design. Birds were presented with two calls from either one or two species. In both experiments, there were four alarm treatments: 1) two overlapping calls from scrubwrens (A) or fairy-wrens (B), 2) two overlapping calls from crimson rosellas (A & B), 3) one call from a scrubwren (A) or fairy-wren (B) followed by one call from a crimson rosella (A & B), 4) one call from a crimson rosella (A & B) followed by one call from a scrubwren (A) or fairy-wren (B).This resulted in a blocked design, in which I could look at the effect of both the number of species calling (1 & 2 vs 3 & 4) and the order in which the species called (1 & 3 vs 2 & 4). Control playbacks were constructed in the same way using contact calls from the species instead. In order to minimize the number of playbacks presented, birds only received two control treatments, such that they were presented with one control playback from one species (1 or 2) and one control playback from two species (3 or 4).*

If honeyeaters perceive information derived from independent sources as more reliable, they should respond more strongly to the mixed alarm treatments than to the single species alarm playbacks in both experiments. If the reliability of the calling species matters most, they should show greater responses to the scrubwren alarm calls than to the rosella alarms.

Statistical analyses

The number of species calling and the species that called first were included as fixed effects in the models looking at both the fleeing response and at the duration of response.

Results

The number of calling species had no effect on the probability of fleeing to cover (Table 5.4a, p 139). The birds fled to cover almost 100% of the time if the scrubwren was the first species to call, but they only fled about half the time if the rosella call came first, suggesting that the order in which the species were presented is important in determining their responses (Table 5.4a; Fig. 5.7a, p 140). Furthermore, honeyeaters took about three times as long to resume feeding following playbacks composed of two scrubwren calls compared to playbacks made up of two rosella calls (Table 5.4b; Fig. 5.7b). Yet they took an intermediate, and similar, time to return to feeding when presented with calls made up of both a scrubwren and a rosella alarm, regardless of which species called first (Table 5.4b). Females responded for about twice as long to alarm calls compared to males (Table 5.4b; Fig. 5.7c). Neither the identity of the first species to call nor the number of species calling affected the latency to respond to the alarm calls (Table 5.4c)

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Rosella vs Scrubwren (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		0.97±0.69			
		Number (Two)	One	-1.13±0.66	1	3.24	0.07
		First to call (CR)	SW	3.60±1.01	**1**	**27.61**	**<0.0001**
		Sex (Female)	Male	-0.39±0.78	1	0.26	0.61
	Dropped terms	Number:First to call (Two:CR)	One:SW	1.38±1.67	1	0.67	0.41
	Random term	*Bird - variance*		1.30			
(b) Rosella vs Scrubwren (LMM)	**Duration of response**						
		(Intercept)		7.01±0.37			
		Sex (Female)	Male	-0.66±0.29	**1**	**4.66**	**0.03**
		Order (First)	Second	-0.23±0.34	5	9.50	0.09
			Third	-0.53±0.35			
			Fourth	-0.33±0.35			
			Fifth	-0.81±0.32			
			Sixth	-0.69±0.32			
		Number:First to call (Two:CR)	One:SW	1.24±0.37	**1**	**11.76**	**0.0006**
	Random term	*Bird - variance*		0.30			
		Playback set- variance		0.18			
(c) Rosella vs Scrubwren (LMM)	**Latency to respond**						
		(Intercept)		1.41±0.21			
		Number (Two)	One	0.05±0.13	1	0.20	0.66
		First to call (CR)	SW	0.12±0.13	1	0.99	0.32
		Sex (Female)	Male	0.07±1.67	1	0.17	0.68
		Order (First)	Second	-0.13±0.22	5	4.49	0.48
			Third	0.06±0.23			
			Fourth	0.01±0.24			
			Fifth	0.21±0.22			
			Sixth	0.26±0.22			
	Dropped terms	Number:First to call (Two:CR)	One:SW	0.07±0.26	1	0.09	0.77
	Random term	*Bird - variance*		0.07			
		Playback set- variance		0.00			

Table 5.4. *Calling by Heterospecifics Playback Experiment 1 – when one species is more reliable: Outcomes of generalised linear mixed effects models (GLMM) and linear mixed effects models (LMM) to investigate a) the effects of the number of species on the probability of fleeing to cover, b) the effects of the number of species on the duration of response, and c) the effects of the number of species on the latency to respond. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

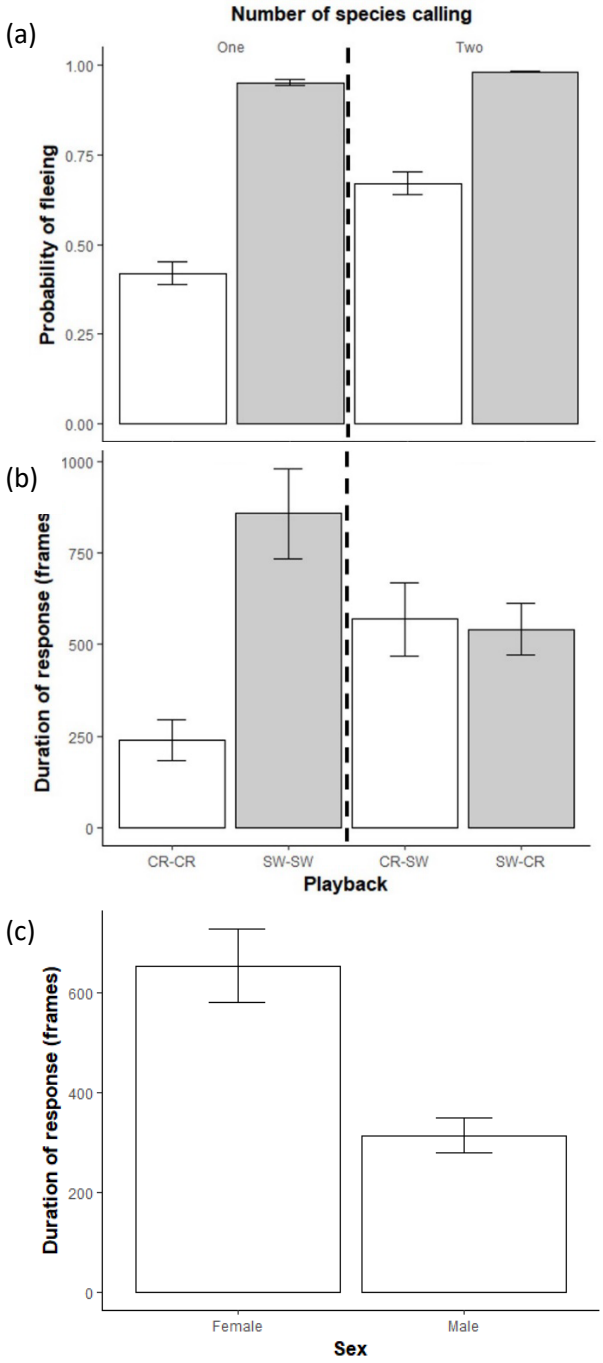


Figure 5.7. *Heterospecific Playback Experiment 1 – one species is more reliable: a) Probability of fleeing to, b) the duration of response, and c) the duration of response in relation to the sex of the focal bird. Fitted values show. 1 frame = 20 ms. Columns represent means. Bars represent standard errors. N = 24 birds. CR stands for crimson rosella. SW stands for white-browed scrubwren.*

b) Heterospecific Playback Experiment 2: both species are unreliable

Methods

In the second experiment, I presented birds with two potentially unreliable sources of information: fairy-wren and rosella alarm calls. The experimental design followed the structure outlined above, but all scrubwren calls were replaced with calls from superb fairy-wrens (Fig. 5.6). Calls were presented at the natural amplitudes of the calling species, such that all fairy-wren calls were calibrated to 57.5 dB at 6 m and all rosella calls were calibrated to 65.5 dB at 6 m.

If honeyeaters perceive information derived from independent sources as more reliable, they should respond more strongly to the mixed alarm treatments than to the single species alarm playbacks in both experiments. As both species are likely unreliable signalers of aerial predators, it is not clear to which species the honeyeaters should respond most strongly.

Statistical analyses

For the two playback experiments, the number of species calling and the species that called first were included as fixed effects in the models looking at both the fleeing response and at the duration of response.

Results

Both the number of species calling and the identity of the species to call first within a playback had significant effects on the honeyeaters' response to the alarm calls (Table 5.5, p 142). Playbacks that consisted of both species calling together prompted over 75% birds to flee, whereas birds fled about 60% of the time on average to single species playbacks (Table 5.5a; Fig. 5.8a, p 143). Two species calling together resulted in birds taking more than twice as long to resume feeding than playbacks comprised of two calls from a single species (Table 5.5b; Fig. 5.8b).

The order in which the species called also affected the honeyeaters' responses. The honeyeaters were both more likely to flee to cover and maintained their response for longer if the fairy-wren alarm call came first than if the rosella was the first to call (Table 5.5a, b; Fig. 5.8). They responded over 60 ms more slowly to alarm playbacks in which the fairy-wren called first (Table 5.5c; Fig. 5.8c).

Model	Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests		
			Factor levels	Effect ± SE	df	LRT χ^2	p
(a) Rosella vs Fairy-wren (GLMM)	**Probability of fleeing to cover**						
		(Intercept)		0.40±0.65			
		Number (Two)	One	-1.14±0.57	**1**	**4.49**	**0.034**
		First to call (CR)	FW	1.64±0.60	**1**	**9.00**	**0.0027**
		Sex (Female)	Male	0.83±0.79	1	1.13	0.29
	Dropped terms	Number:First to call (Two:CR)	One:FW	0.83±1.10	1	0.58	0.45
	Random term	*Bird - variance*		1.83			
(b) Rosella vs Fairy-wren (LMM)	**Duration of response**						
		(Intercept)		7.01±0.37			
		Number (Two)	One	-0.64±0.26	**1**	**6.64**	**0.01**
		First to call (CR)	FW	0.66±0.26	**1**	**6.57**	**0.01**
		Sex (Female)	Male	0.39±0.27	1	2.10	0.15
		Order (First)	Second	-0.10±0.45	5	8.83	0.12
			Third	-0.95±0.44			
			Fourth	-0.45±0.45			
			Fifth	-0.76±0.47			
			Sixth	0.04±0.45			
	Dropped terms	Number:First to call (Two:CR)	One:FW	0.06±0.52	1	1.57	0.21
	Random term	*Bird - variance*		0.05			
		Playback set- variance		0.09			
(c) Rosella vs Fairy-wren (LMM)	**Latency to respond**						
		(Intercept)		1.74±0.18			
		Number (Two)	One	-0.01±0.12	1	0.01	0.94
		First to call (CR)	FW	0.37±0.12	**1**	**9.70**	**0.0018**
		Sex (Female)	Male	0.09±0.12	1	0.68	0.41
		Order (First)	Second	0.12±0.21	5	3.74	0.59
			Third	0.09±0.20			
			Fourth	0.26±0.21			
			Fifth	0.28±0.22			
			Sixth	-0.01±0.21			
	Dropped terms	Number:First to call (Two:CR)	One:FW	-0.03±0.25	1	0.02	0.90
	Random term	*Bird - variance*		0.00			
		Playback set- variance		0.01			

Table 5.5. *Calling by Heterospecifics Playback Experiment 2 – when both species are unreliable: Outcomes of generalised linear mixed effects models (GLMM) and linear mixed effects models (LMM) to investigate a) the effects of the number of species on the probability of fleeing to cover, b) the effects of the number of species on the duration of response, and c) the effects of the number of species on the latency to respond. The means estimates ± S.E. are presented for fixed effects, variances are presented for random effects. The p-value for each term is derived from a likelihood ratio test for changes in deviance when models with that term and without it are compared. Terms in bold resulted in a significant change in deviance when removed from the model.*

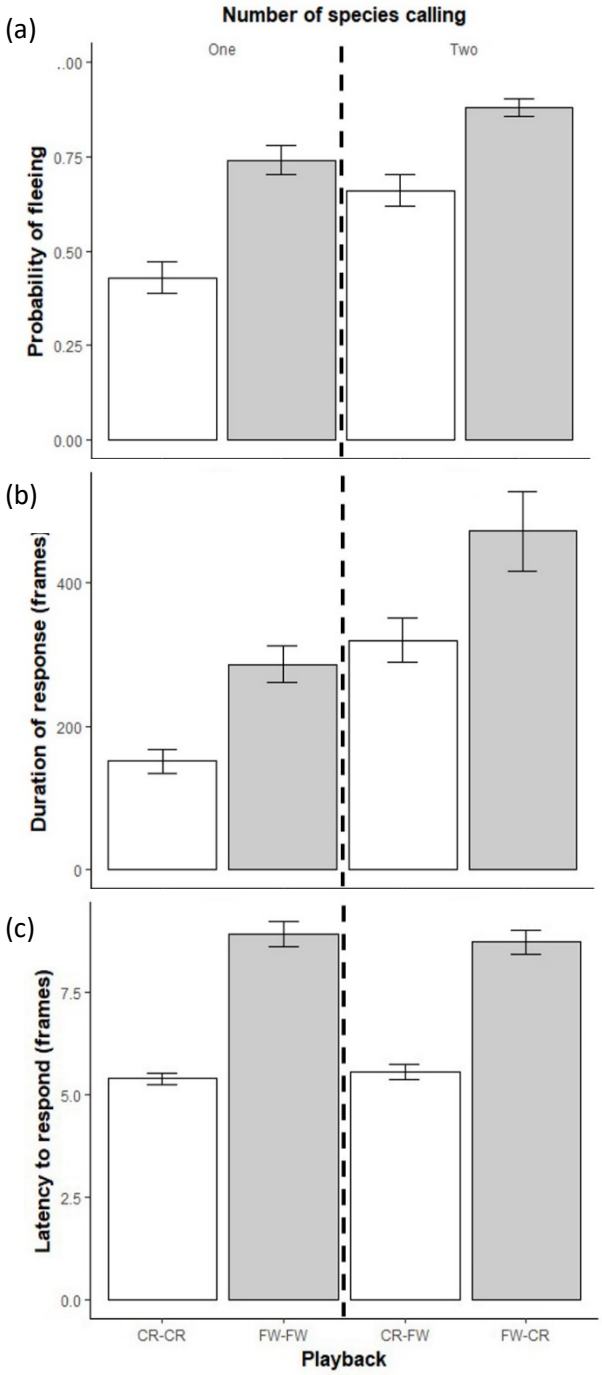


Figure 5.8. *Heterospecific Playback Experiment 2 – both species are unreliable: a) Probability of fleeing, b) duration of response, and c) latency to respond to playbacks. Fitted values shown. 1 frame = 20 ms. Columns represent means. Bars represent standard errors. N = 24 birds. CR stands for crimson rosella. FW stands for superb fairy-wren.*

5.8 DISCUSSION

When presented with multiple sources of information about danger, honeyeaters attended to the number of signalers but adjusted their responses according to the reliability of the sources. They did not respond more strongly to two alarm calls from a single individual than to one call from the same bird. However, they were both more likely to flee and slower to resume feeding following alarm calls from two conspecifics than after two calls from one caller. Their assessment of information derived from heterospecifics was more complicated: they showed stronger responses to a mixed species chorus than to calls from a single species when the two participating species were both unreliable, but their behaviour was determined by the order in which the species called when one of the heterospecifics was more reliable than the other.

Conspecific information

Honeyeaters appear not to attend to the number of calls when using conspecific information, even though repeated signals from one caller were a reliable sign of greater danger. Flying sparrowhawks were associated with multiple calls from a single individual, but honeyeaters were no more likely to flee and showed no significant difference between the time to resume feeding after playbacks of two alarm calls than after one alarm from a single individual. Honeyeaters that did not flee to the first call usually showed information-seeking behaviours instead, such as scanning for danger. As the social information provided by the single caller conflicted with their personal information, which indicated the absence of danger, these birds generally did not flee to the second call. While more than one call from a single caller may be a relatively consistent indication of danger, honeyeaters do not appear to treat it as such, instead devaluing additional information originating from a single source.

Honeyeaters did, however, value the number of conspecific callers over the number of calls alone. Dangerous predators were three times more likely to prompt multiple individuals to call than less threatening stimuli, suggesting that multiple callers reliably signal danger. This supports the prediction of theoretical models that overall accuracy of social information increases with the number

of informants (Codling et al., 2007; Lima, 1994; Sumpter & Pratt, 2009; Wolf et al., 2013). Consistent with the pattern found in natural predator encounters, honeyeaters showed significantly stronger responses to alarm calls from two individuals than to calls from one, suggesting that birds value information derived from multiple sources more highly.

Evidence that animals are sensitive to the number of informants when making decisions is widespread among vertebrates (Benson-Amram et al., 2011; Bousquet et al., 2011; Robert, 1997; Sumpter et al., 2008; van Belle & Scarry, 1998; Wolf et al., 2013). For example, both Richardson's ground squirrels, *Spermophilus richardsonii*, and yellow-bellied marmots, *Marmota flaviventris*, spent less time feeding when exposed to alarm calls from multiple individuals (Blumstein et al., 2004b; Sloan & Hare, 2008). Interestingly, I found that the playbacks with two callers occasionally prompted the focal birds to give alarm calls themselves, a behaviour that was unique to this experiment. Such contagious calling can lead to information cascades rapidly spreading potentially erroneous social information through the population (Giraldeau et al., 2002). However, contagious calls were given on less than 10% of occasions, suggesting that this may be a rare occurrence. Nonetheless, it is consistent with the idea that birds perceived two conspecifics calling simultaneously to be a good indicator of predator presence. The rarity of contagious calling reinforces the idea that two individuals normally provide independent information, rather than merely reflecting a cascade of social information. Overall, then, while both the number of calls and the number of callers appear to be reliable signs of high risk situations, the honeyeaters only adjusted their responses according to the number of independent signals.

It is not clear whether New Holland honeyeaters are able to recognise individual callers by voice alone and accrue the benefits of vocal recognition. In this study, the honeyeaters responded more strongly to playbacks consisting of two callers rather than a single caller, but only significantly so when the playbacks also differed in the location of the callers and the calls overlapped, an unambiguous cue of multiple callers. Whether the calls came from one or two locations did not appear to be a sufficient cue that the honeyeaters used when determining the number of callers. Acoustic

variation alone also did not appear to be sufficient for numerical assessment, as there were no significant differences in the responses of birds to playbacks of one and two callers when both were presented from two locations and without overlap. But the honeyeaters took almost twice as long to resume feeding following two consecutive callers compared to the two single caller treatments, though the difference was not significant. Even overlapping calls alone did not provide a clear mechanism for numerical assessment, as birds showed no difference in response between playbacks consisting of two callers with consecutive or overlapping calls. However, the fleeing responses of the birds did appear to increase in a linear fashion with each additional cue of multiple callers, and the duration of response was also longer with each cue, so it is possible that birds are using all of the cues together to assess the number of callers rather than relying on one alone.

Assessing the number of callers by recognising individuals could bring other advantages, such as evaluating individual reliability. There is evidence for sufficient variation in alarm calls between individuals and consistency within individuals to allow for individual recognition of alarm callers in a range of birds and mammals (Blumstein & Munos, 2005; Couchoux & Dabelsteen, 2015; Leuchtenberger et al., 2016; Randall et al., 2005; Schibler & Manser, 2007; Schneiderová & Policht, 2011; Sproul et al., 2006; Yorzinski, 2014), and playback experiments to several of these species have demonstrated that some are indeed able to discriminate between individuals (Blumstein & Daniel, 2004; Cheney & Seyfarth, 1988; Colombelli-Négrel & Evans, 2017; Hare, 1998; Nichols & Yorzinski, 2016; O'Connell-Rodwell et al., 2007; cf. Schibler & Manser, 2007). As individuals may differ in their reliability, vocal recognition of alarm callers would enable receivers to adjust their responses according to the likely validity of the specific caller, as has been found in North American sciurids and vervet monkeys, *Cercopithecus aethiops* (Blumstein et al., 2004b; Cheney & Seyfarth, 1988; Hare & Atkins, 2001).

Heterospecific information

New Holland honeyeaters appear to pay attention to the number of species when eavesdropping on the alarm calls of multiple heterospecifics. The observational data revealed that over 75% of alarm choruses given to sparrowhawks, a dangerous predator of small birds, included more than one species calling, whereas this figure was less than 10% for wattlebirds, a nonpredatory species (Higgins et al., 2001; Marchant & Higgins, 1993). This finding suggests that multi-species choruses are a good sign that a predator is present. More species calling could also indicate a more dangerous predator, as choruses were more likely to contain multiple species when the prompt was a sparrowhawk than when it was the opportunistic currawong.

Accordingly, when presented with calls from crimson rosellas and superb fairy-wrens, birds were both more likely to flee and delayed feeding for longer following playbacks containing alarm calls from both species compared to playbacks of each species alone. Crimson rosellas are about 6 to 8 times the size of New Holland honeyeaters and seem to produce a single, general alarm call to ground threats, like dogs, and flying raptors, including wedge-tailed eagles that are not a threat to honeyeaters (Higgins, 1999; personal observation). As such, their alarm call is unlikely to be a reliable indicator that birds should flee to cover. Consistent with this, honeyeaters only fled less than half the time to rosella alarm calls alone. Fairy-wrens are smaller than honeyeaters and, while they have a specific call for aerial threats, they give a high number of false alarm calls to non-predators (Magrath et al., 2009a). Previous research has found that honeyeaters may treat their calls as unreliable (Magrath et al., 2009a), and in this study the birds fled less than 75% of the time to two fairy-wren callers. However, when fairy-wrens and crimson rosellas alarm call together, the prompt is likely to be in flight and something that threatens both species, as well as the honeyeaters, like a sparrowhawk. As a result, the honeyeaters showed stronger responses to the mixed chorus, fleeing over 80% of the time and spending more time in cover than to either species alone. From the honeyeaters' perspective, the combination is greater, in terms of reliability, than the sum of its parts.

Honeyeaters may use simple numerical rules when eavesdropping on multi-species choruses of species with comparable reliability, but this finding was not supported when there was a large disparity in the relative reliability of the participating species. Unlike rosellas, white-browed scrubwrens have an aerial alarm call and call to nonpredators less than 20% of the time (Magrath et al., 2009a). Honeyeaters fled to their alarm calls almost 100% of the time in this experiment, whereas they fled only about 35% of the time to rosella alarms alone. But when the scrubwren alarm calls were presented after rosella calls, the honeyeaters were less likely to flee. Furthermore, they spent the greatest amount of time in cover after playbacks of scrubwren alarms alone, and an intermediate amount of time in cover after the mixed-species playbacks. This is similar to the findings of a study on green frog, *Rana clamitans*, tadpoles, which showed a graded response to heterospecific and conspecific chemical cues of danger (Fraker, 2009). They responded most weakly to the heterospecific cues alone, responded at an intermediate level to the treatment with a mixture of conspecific and heterospecific cues, and maintained their response for longest to conspecific cues alone, probably because conspecific information is likely to be more accurate. It therefore seems that where there is a significant discrepancy in the relative reliability of the two sources of information, individuals show an intermediate level of response when the sources are combined.

As New Holland honeyeaters make very rapid decisions about danger (Chapter 3), the order in which the heterospecific species called was of particular importance in determining the honeyeaters' responses. There was considerable variation in the order of calling during natural multi-species alarm choruses: honeyeaters were the first to call over 60% of the time and scrubwrens around 50% of the time, whilst crimson rosellas and superb fairy-wrens called first in only about 25% of choruses in which they participated. This could reflect differences in detection abilities, as the honeyeaters use exposed perches and may consequently be quicker to spot oncoming threats than ground-feeding fairy-wrens (Greig-Smith, 1981; Martínez & Zenil, 2012; Radford et al., 2009). In both multi-species playback experiments, the honeyeaters were less likely to flee to playbacks in which the less reliable species, the crimson rosella, called first. Honeyeaters make split-second decisions over

fleeing (Chapter 3) and they value their personal information above social information from conspecific alarm calls (Chapter 4). As the rosella alarm calls were rarely ignored and prompted scanning in birds that did not immediately flee, these birds would have acquired some personal information by the time the second, more reliable species began calling. Since no threat was actually present, the honeyeaters' reliance on personal over social information can account for the reduction in flees to cover and the importance of the order of calling.

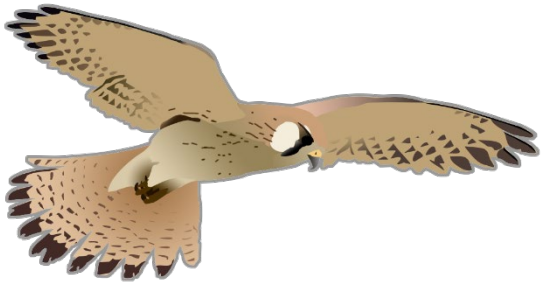
Honeyeaters took much longer to react to the alarm calls of superb fairy-wrens than to the calls of the other heterospecifics. The delay from the onset of the playback to the start of a response was almost 220ms when a fairy-wren called first. This is a significant delay, as an attacking hawk could travel around 5m in that time (Goslow, 1971; Hilton et al., 1999), and honeyeaters have generally already initiated their escape flight in this time when responding to conspecific alarm calls (Chapter 3). Fairy-wren alarm calls have a much higher peak frequency (9.1 kHz) than honeyeater alarms (3.6 kHz), so it is possible that honeyeaters could have trouble hearing their calls (Magrath et al., 2009a). Birds generally show lower sensitivity at frequencies above 5 kHz, a threshold that encompasses the peak frequency of honeyeater alarm calls but is greatly exceeded by the 9 kHz peak frequency of fairy-wren alarms (Magrath et al., 2009a; Okanoya & Dooling, 1987). Furthermore, birds can find it more difficult to discriminate between heterospecific than conspecific calls, and fleeing responses to heterospecific alarm calls are disproportionately reduced when the signal is degraded (Dooling et al., 1992; Lohr et al., 2003; Murray & Magrath, 2015). Sensory constraints could therefore reduce the value of heterospecific information or make it slower to gain information (Magrath et al., 2015a).

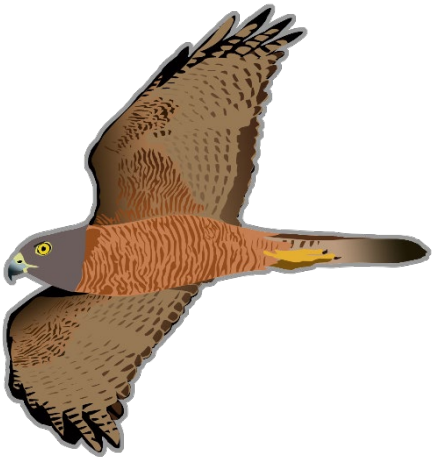
Conclusions

I show that birds do pay attention to the number of callers when assessing social information derived from both conspecifics and heterospecifics. By using information from multiple sources, individuals can improve their likelihood of successfully detecting danger, making the most of the "many eyes" watching out for threats in the community. At the same time, they can moderate their responses according to simple rules about the number of callers to reduce the risk of fleeing to false

alarms: information derived from a greater number of independent sources, such as two conspecific callers or two different species, should be valued over information coming from a single source. Honeyeaters did follow this rule when the two sources of information were similarly reliable. However, differences in detection abilities and alarm calling propensity between species means that natural alarm choruses may not contain equally reliable participants (Goodale et al., 2010). As a result, applying simple rules indiscriminately may not be the most adaptive solution for eavesdroppers. My results suggest that when presented with a mixed-species chorus with a large disparity in heterospecific reliability, eavesdroppers adjust the weighting of the information to reflect the reliabilities of the calling species and respond at an intermediate level. By combining simple numerical rules with reliability weightings, animals can efficiently exploit the rich and varied information available to them from the local prey community's neighbourhood watch.

Chapter 6





General Discussion

It is no mere coincidence that as my fluency in the alarm calls of New Holland honeyeaters, *Phylidonyris novaehollandiae*, grew, so too did my encounters with previously elusive avian predators. Time taught me to listen out for clues of the source of alarm in the number of elements or the number of callers, the very same information the birds themselves use, and once-unguided scans of the surroundings were refined, once-unseen threats now detected. The pattern of calling, so familiar in its association with grey butcherbirds, *Cracticus torquatus*, in the botanic gardens, was the same sound that revealed a butcherbird to us on a coastal hike 300 km away. It was the tattle-tale chatter of a honeyeater that alerted eavesdropping heterospecifics, myself amongst them, to a pied currawong, *Strepera graculina*, systematically disemboweling a European blackbird, *Turdus merula*. No stealthy fox with a mouthful of possum nor frogmouth-clasping goshawk can slip through the gardens undetected if there is a honeyeater on watch nearby. Should you wish to see a big-eyed boobook, *Ninox novaeseelandiae*, observe a hovering nankeen kestrel, *Falco cenchroides*, watch the heart-stopping, high-speed hunt of a peregrine falcon, *Falco peregrinus*, or avoid a foot falling fatally upon a brown snake, *Pseudonaja textilis*, there is no better language to learn than that of the honeyeater alarm calls. You need only ask the other birds.

In this concluding chapter, I provide an overview of the key findings from this thesis before discussing possible avenues for future research.

6.1 Production of alarm calls

The contexts in which alarm calls are produced and the information that they convey are important for determining the sort of information that is available to both the intended receivers of the signals and eavesdropping heterospecifics. Different species can encode different aspects of predation risk in their alarm calls, such as indicating the type of predator, its behaviour, or its proximity to the caller (Griesser, 2008; Leavesley & Magrath, 2005; Suzuki, 2011). The specific information communicated by each species in a community will shape the local communication network, resulting in a resilient network if the information provided by different species is redundant, and a diverse one

if species convey complementary information by signaling about different attributes of predators (Magrath et al., 2015a). Thus, investigating the production of alarm calls is an important step in understanding information transfer within communities.

In Chapter 2, I showed that New Holland honeyeaters use their whistle alarm call when in the presence of flying threats, both during natural encounters and when presented with gliding model predators. Such aerial alarm calls may be particularly important sources of information, as hunting raptors represent a serious danger for small birds. Raptor predation has been estimated to be responsible for 10 to 50% of the annual mortality in some bird populations (Cresswell & Whitfield, 1994; Lindström, 1990). Consistent with this, honeyeaters take immediate evasive action when presented with the aerial alarm calls of conspecifics (Chapter 3; Magrath et al., 2009).

The alarm calls of New Holland honeyeaters do not simply indicate the presence of an aerial predator. In Chapter 3, I found that honeyeaters also encode urgency information in their aerial alarm calls. The honeyeaters included a greater number of elements in alarm calls that were given to more dangerous predators. Furthermore, honeyeaters were more likely to flee and spent more time in cover following playbacks of alarm calls with more elements. Communicating graded information through the number of elements appears to be a common signaling strategy amongst birds (Fallow & Magrath, 2010; Martínez et al., 2017; Suzuki, 2016; Templeton et al., 2005), presumably because this strategy reduces the risk of errors (Leavesley & Magrath, 2005). Yet individuals must respond rapidly to hunting hawks if they are to evade capture (Goslow, 1971; Lind et al., 2002; Malmiga et al., 2014; van der Veen & Lindström, 2000). I showed that a multi-element alarm call also conveys sufficient information about the degree of danger in the acoustic structure of the first element of the call, such that receivers can accurately assess the degree of risk even if they only hear the first element. My video recordings of the responses revealed that birds flee to alarm calls in under a quarter of a second, a necessarily rapid response for avoiding a flying predator. As few previous studies have considered the speed of response to alarm calls, it is not yet clear how widespread this signaling mechanism might be.

The information provided by the alarm calls of New Holland honeyeaters may be especially valuable to other species in the local prey community. Species can differ in their ability to detect threats and vary in the likelihood of calling when faced with a predator (Goodale & Kotagama, 2005a; Martínez et al., 2017). Species that are particularly good at spotting predators and communicating about them may become "keystone" species in interspecific communication networks (Goodale et al., 2010; Magrath et al., 2015a; Martínez et al., 2017). In mixed-species foraging flocks, species that feed high in the canopy and hawk for insects often take on the role of sentinel species, providing reliable information about danger, due to their increased likelihood of detecting predators (Goodale & Beauchamp, 2010; Martínez & Zenil, 2012). On average, male honeyeaters spend around 40 minutes of every hour perched out of cover, where they have a good view of their surroundings and could function as community sentinels (Chapter 2; Magrath et al., 2015). While honeyeaters do not form foraging flocks with ground-feeding species, their aerial alarm calls are very loud and could be easily detected by birds some distance away (Higgins et al., 2001). Furthermore, male honeyeaters called over 70% of the time when they were presented with models of a dangerous predator, which suggests that they have a high propensity to call when they detect threats (Chapter 2 & 3). Consistent with the possibility that New Holland honeyeaters may serve as a sentinel species, a wide range of species has been reported to attend to their alarm calls, making the information their calls convey important to the community at large (Igic et al., 2015; Jurisevic & Sanderson, 1994a; Magrath et al., 2009a; Rooke & Knight, 1977).

6.2 USE OF SOCIAL INFORMATION ABOUT DANGER

Animals potentially have access to several sources of information about threats in their environment, as they can detect predators directly themselves, attend to the behaviour of knowledgeable conspecifics or eavesdrop on the alarms of heterospecifics (Magrath et al., 2015a; Schmidt et al., 2010). Indeed, individuals may even have simultaneous access to both personal and social information about a predator, or hear a chorus of alarms from multiple individuals and species

calling together to the same threat. Yet few studies explicitly place avian alarm calling in the context of information use, and most playback experiments consider only a simple signaler-receiver dyad, avoiding the complications of including multiple signalers (McGregor, 2005). As such, our understanding of how individuals integrate and value information in the face of danger is limited. In the second half of my thesis, I attempted to address these issues by examining how the amount of information and the quality of the information affect its use.

In Chapter 4, I found that New Holland honeyeaters value their personal information about danger above social information from alarm calls, despite the potentially fatal context. Across the experiments, birds fled to cover in response to alarm playbacks less than 25% of the time when they were perched out of cover and could see that no predators were present, disregarding the conflicting social information from alarm calls. In contrast, foraging birds fled over 50% of the time when presented with alarm playbacks in this chapter, demonstrating that receiver behaviour can affect their reliance on social information. When honeyeaters were presented with two consecutive alarm calls from a single conspecific in Chapter 5, they never fled in response to the second alarm if they had already scanned to the first call. As these individuals will have acquired additional personal information by scanning, this is consistent with the finding that honeyeaters value their own information more highly than information from others. Given that the cost of ignoring a true alarm could be injury or death, one might expect all receivers to play it safe, as the foraging honeyeaters do, and respond to alarm calls even if they cannot see the threat. However, the trade-off between personal and social information shown by New Holland honeyeaters is similar to findings from studies of information use in other contexts, where knowledgeable individuals value what they themselves know over conflicting information derived from others (Cronin, 2013; Heinen & Stephens, 2016; van Bergen et al., 2004).

Favouring personal information over social information should reduce the likelihood of information cascades being propagated by uninformed individuals (Dall et al., 2005; Giraldeau et al., 2002). While information cascades, in which the behaviour of others overrides an individual's personal

information, may often be correct, errors can occur if the initiating individuals make a mistake (Giraldeau et al., 2002). The accuracy of social information will be maintained if individuals, like the perched honeyeaters, integrate it with their personal information before responding or if uninformed individuals value the social information according to the number of independent signals (Giraldeau et al., 2002; Sumpter & Pratt, 2009). The potential for erroneous information cascades appears to be low in New Holland honeyeaters. Across my thesis, there were only 5 occasions out of over 500 playback presentations of conspecific alarm calls on which playbacks prompted the focal honeyeater to produce an alarm call itself, demonstrating that it is a very rare occurrence. All five instances involved playbacks of two alarm calls and four of the playbacks were comprised of two individuals calling, suggesting that cascades might only arise if a threshold number of signalers is crossed.

As well as adjusting their responses to the amount of personal information available, I found that honeyeaters also paid attention to the number of independent sources of social information. In Chapter 5 I showed that honeyeaters were both more likely to flee and stayed in cover for longer following the presentation of two alarm calls from two different conspecifics than after two calls from a single individual. They were also attentive to the number of calling species when assessing information from two similarly reliable (or, in this case, unreliable) species. Honeyeaters fled more frequently and took longer to resume feeding after hearing two alarm calls from two different species than after two calls from one species. Quorum rules have been described in groups that require consensus to coordinate collective movement, such as in African wild dogs, *Lycaon pictus*, and meerkats, *Suricata suricatta*, where at least three individuals need to have sneezed or vocalised, respectively, to facilitate group movement (Bousquet et al., 2011; Walker et al., 2017). In such instances, a threshold number of signalers is required to trigger an all-or-nothing response. For honeyeaters, however, the number of conspecific callers and calling species affected their behaviour in a more graded way, with more signalers increasing the magnitude of the response.

To the ears of a New Holland honeyeater, not all alarm calls are equal. Across both Chapter 4 and 5, I found that honeyeaters were sensitive to the quality of the information with which they were

presented. They were less likely to flee to conspecific alarms that had been degraded and attenuated, cues associated with the sound travelling a greater distance (Naguib & Wiley, 2001). Birds that are further from the caller may perceive the signal as less urgent, indicative of a more distant predator, and may consequently choose to first gather additional personal information before deciding whether to flee. Furthermore, the alarm calls of other species were treated as a less relevant, or reliable, sign of danger, prompting fewer flees than conspecific calls. When eavesdropping on a heterospecific alarm chorus, the honeyeaters paid attention to the relative reliability of the participating species. If there was a large disparity in the reliability of the two species, their fleeing response was determined not by the number of calling species but by whether or not the more reliable species called, a pattern similar to stimulus dominance in the signal design literature (Munoz & Blumstein, 2012; Partan & Marler, 2005). In both chapters, I found evidence to suggest that some heterospecific alarm calls may be harder to detect or process than conspecific calls. Honeyeaters took longer to respond to the high-frequency alarm calls of white-browed scrubwrens, *Sericornis frontalis*, and the superb fairy-wren, *Malurus cyaneus*, than to their own alarms. This suggests that listening to acoustically dissimilar heterospecific alarm calls may make it slower to gain information, a potential disincentive to rely on other species when facing a fast-moving predator.

6.3 SEX DIFFERENCES

An unexpected discovery from my research was the importance of sex in determining the antipredator behaviour of New Holland honeyeaters. Reports on sex-biased alarm production are not common, but it is not clear whether this is because sex-biased alarm calling is itself rare or whether few studies take sex into consideration in the context of alarm production. In species that produce low amplitude, high-frequency aerial alarm calls, it may well be difficult to determine which individual called. The loud and conspicuous calling by individual honeyeaters, on the other hand, made it relatively easy to identify the caller and to investigate the occurrence of sex-biased alarm calling. In Chapter 2, I found that male honeyeaters were far more likely to produce aerial alarm calls than

females, both during natural observations and when presented with model predators. Although male honeyeaters spent more time perched and may therefore be more likely to see threats, there appear to be fundamental differences in the propensity to call upon detecting a predator. The discrepancy in the propensity to call was found to exist across seasons, as male birds were also more likely to give alarm calls when presented with model predators outside of the spring breeding season in Chapter 4. In that experiment, the thrower was blind to the sex of the bird during presentations, so the sex differences are unlikely to be due to bias in the manner of the presentations.

While male honeyeaters appear to be the primary producers of alarm calls, female honeyeaters seem to be the main consumers of the information. Although the difference was not always significant, females fled to cover more frequently than males in 8 of the 9 playback experiments I carried out. Overall, females fled to around 57% of conspecific alarm playbacks, whereas males fled to less than 40%. Female honeyeaters also took about 5 s longer on average to resume feeding after honeyeater alarm calls than males across the experiments (female mean ± SE: 23.02 s ± 0.33; male mean ± SE: 17.72 s ± 0.25). At other study sites in Australia, a male-biased sex ratio has been reported in honeyeater populations due to higher female mortality (Higgins et al., 2001), which suggests that females may be at greater risk than males. Birds are sensitive to their vulnerability: male superb fairy-wrens are more likely to flee to alarm calls and stay in cover for longer when adorned in their eye-catching blue breeding plumage than when in their winter brown (McQueen et al., 2017). The stronger response of female honeyeaters to alarm calls could therefore be a result of their greater vulnerability. Alternatively, female honeyeaters spend considerably less time perched and vigilant than male honeyeaters, which look out for, and defend the territory against, conspecific intruders and heterospecific competitors (Paton, 1985; Recher, 1977). This likely results in females having less personal information about danger and consequently relying more on social information from alarm calls (Rosa et al., 2012).

The chapters of this thesis have thus revealed some of the complex decision-making behind a simple fleeing response. Honeyeaters are able to make rapid assessments of the degree of danger

they face by attending to the signal urgency, source and number. They can integrate the information that they extract from alarm calls with their own personal information and vulnerability to make flexible decisions about the threats in their environment.

6.4 FUTURE WORK

It is striking that after many decades of research on alarm calls, we still understand so little about *why* individuals give these calls. Despite implicit references in the literature to the cost of calling, there is little empirical evidence to support this assertion (Kareksela et al., 2013; Klump et al., 1986; Sherman, 1985; Sullivan, 1985). In fact, there is a conspicuous paucity of empirical research on this subject entirely, likely arising from the difficulties in addressing questions from the perspective of the predators (Boal et al., 2010; Cresswell, 1996; Lima, 2002). But it is important that we do tackle this issue and grapple with the possible costs and benefits that might arise from signaling in the face of danger, rather than relying on mere assumption. The unanticipated discovery of sex-biased production of alarm calls by New Holland honeyeaters simply highlights the fact that the selective pressures on alarm calling may differ between classes of individuals within a species, and recent work on personality suggests that variation in the particular traits of individuals could impact the trade-off between calling and staying silent (Guillette & Sturdy, 2011; Hyman et al., 2013). Even the location of the individual could affect the cost: male honeyeaters seem to preferentially call from a perched position. Furthermore, the loud, low, conspicuous alarm calls of Australian honeyeaters contrast with the classic “seeet” calls of species like the European blackbird (Marler, 1955). These clear structural differences suggest an avenue for comparative work to define the different selective pressures between species that gave rise to such marked variation in signaling strategies. There are several levels, from individual to species, at which the costs and benefits of alarm calling could differ, but we need much more knowledge on how alarm calls influence predator behaviour and the long-term survival of callers and their relatives to understand the evolution of these warning signals.

In my thesis, I hope to have demonstrated that there is much to be gained by considering alarm calls in the context of information use, and that these signals provide a wonderful opportunity to deviate from the traditional signaler-receiver dyad in favour of exploring networks of information with multiple signals and signalers. There is growing interest in viewing the information exchange between individuals as part of a communication network that extends across species (McGregor, 2005; Snijders & Naguib, 2017), and alarm calls would make for an excellent study system. The potential receivers that could benefit from listening to alarm calls include any individuals within earshot – conspecifics, heterospecifics and even predators themselves – which enables researchers to look at information use from many different perspectives.

As multiple individuals within or across species can signal at the same time about the same threat, alarm calls allow us to investigate what information individuals extract from multiple signals. It is possible that propagation of an alarm chorus could be used by receivers within the network to infer the movement of a predator (McGregor & Horn, 2015). A study using a microphone array found that individual red-winged blackbirds, *Agelaius phoeniceus*, gave alarm calls when they were ahead of a hunting hawk, went silent as the hawk passed over them, and resumed calling after it had moved beyond them (Bower & Clark, 2005). I have observed a similar "corridor of silence" forming below the predator during honeyeater alarm choruses. It raises intriguing possibilities to explore, such as whether animals use spatiotemporal information from alarm choruses and patterns of sound and silence to assess their current risk in relation to where the predator might be (Thompson & Hare, 2010).

By considering alarm calling behaviour in the framework established for social networks, it should be possible to examine information flow and how it structures communities. In doing so, we can identify the roles that different individuals, classes of individual, or species, play in the transfer of information through the network (McGregor & Horn, 2015). Some species, or individuals, may be particularly good at detecting and signaling about predators, providing information to the network; whereas other members of the network may be information sinks if they have a low propensity for

calling or make many mistakes (Magrath et al., 2015a; McGregor & Horn, 2015). Understanding such relationships within communities could allow us to recognise potential "keystone" species that may act as essential sources of information about danger (Magrath et al., 2015a; McGregor & Horn, 2015). For example, tufted titmice, *Baeolophus bicolor*, are considered a nuclear species in mixed-species foraging flocks in North America (Dolby & Grubb, 1998). When they were experimentally removed from flocks, white-breasted nuthatches, *Sitta carolinensis*, increased their vigilance, showed reduced nutritional condition, and tended to suffer greater mortality (Dolby & Grubb, 1998). Downy woodpeckers, *Picoides pubescens*, which are known to eavesdrop on the titmouse alarm calls, also showed an increase in vigilance following the removal of the titmice (Dolby & Grubb, 1998; Sullivan, 1984). These results suggest that other species usually benefit from the antipredator behaviours of the titmice (Dolby & Grubb, 1998). Therefore, it may be important to protect such keystone species, as their disappearance could be particularly detrimental to other species within the network.

6.5 Final Thoughts

In 2017, for the first time, a highly vocal, highly social and highly aggressive honeyeater species regularly crossed the threshold into the Australian National Botanic Gardens (personal observation). The noisy miner, *Manorina melanocephala*, is larger than New Holland honeyeaters, but, like them, it feeds upon insects and nectar (Higgins et al., 2001). It has been described as a "reverse keystone" species due its significant negative impact on diversity in avian ecosystems in which it occurs (Montague-Drake et al., 2011). This is a cause for some concern, for although miners are native to Australia, they are proving particularly adept at colonising urban environments and are undergoing rapid range expansion (Major & Parsons, 2010). An increase in noisy miner abundance is associated with a decline in small birds in the area, likely due to their aggressive exclusion of perceived competitors from sites with food (Montague-Drake et al., 2011). This is especially true for small competitor species, such as the New Holland honeyeater. Historically, the New Holland honeyeater was the second most frequently recorded species in Sydney bird communities (Major & Parsons,

2010). Now, noisy miners are one of the most common and New Holland honeyeaters no longer make it into the top ten (Major & Parsons, 2010). It is worth noting that when I tried to find sites around the Australian Capital Territory where New Holland honeyeaters were present at the start of my PhD, I only found them in locations where noisy miners were not present. Successful colonisation of the botanic gardens by noisy miners is not likely to bode well for the local New Holland honeyeater population.

Alarm calling information networks may well be somewhat resilient to the loss of one species and its subsequent replacement by another. There is both direct and indirect evidence that birds can learn to recognise novel sounds as alarm calls (Haff & Magrath, 2012; Magrath et al., 2015b; Magrath & Bennett, 2012). For example, superb fairy-wrens in the Australian National Botanic Gardens do not respond to the alarm calls of noisy miners, but fairy-wrens living on the campus of the Australian National University across the road, where noisy miners are common and which is well within the dispersal distance of a fairy-wren, do flee to cover (Magrath & Bennett, 2012). The ability to learn new alarm calls should allow community networks to cope with changes. However, the new species may be a less valuable source of information than the one it replaces. In Sweden, the native pied flycatcher, *Ficedula hypoleuca*, is steadily being displaced by the closely related collared flycatcher, *F. albicollis*, (Wheatcroft et al., 2016). Despite around 60 years of exposure to the replacement species at the study site, heterospecific members of the community responded more weakly to the mobbing alarm calls of the collared flycatcher than to the pied flycatcher, which could adversely impact the community's success at driving off potential predators (Wheatcroft et al., 2016). Similarly, in a study on heterospecific eavesdropping, fairy-wrens tested with New Holland honeyeater alarm calls in the botanic gardens fled to cover 100% of the time, whereas in the miner study, campus fairy-wrens fled under 80% of the time to miner alarm calls (Magrath et al., 2009a; Magrath & Bennett, 2012).

In addition to differences in community response to alarm calls, there can be differences in the sort of information conveyed by the alarm calls of the displaced species and those of its replacement. I have shown in this thesis that New Holland honeyeaters have a specific alarm call for

aerial predators and that they convey urgency in their calls, communicating how dangerous the predator is. They do so in such a way that receivers, and potentially heterospecific eavesdroppers, can make accurate assessments of risk extremely quickly and consequently escape rapidly from any oncoming predator. Noisy miners also give distinct alarm calls to flying predators (Cunningham & Magrath, 2017; Farrow et al., 2017). However, a preliminary experiment found no clear evidence that they encode urgency in their aerial alarm calls (Igic et al., in prep). This suggests that, given the widespread eavesdropping on New Holland honeyeater alarm calls, their disappearance from the botanic gardens could represent a genuine loss in the information available to the community.

The loss or introduction of a single species can have profound and cascading effects on an ecosystem. This has been most famously demonstrated by the astonishing changes wrought by the reintroduction of grey wolves, *Canis lupus*, to Yellowstone National Park (Ripple & Beschta, 2004). By reducing the elk, *Cervus elaphus*, population size and creating a "landscape of fear", the presence of wolves has changed the species assemblages of not only their prey species, but also the plants upon which the elk feed (Ripple et al., 2015). These in turn have resulted in an unforeseen trophic cascade that enabled the recolonisation of the region by beavers, *Castor canadensis*, and reshaped the rivers and their aquatic inhabitants (Beschta & Ripple, 2016; Ripple & Beschta, 2004). The ecology of fear changed a landscape.

The nonlethal effects of predation may be just as important in determining the ecology and population dynamics of communities as direct mortality (Cresswell, 2008; Lima, 1998). Cues of predator presence alone are sufficient to change habitat use, such as beavers avoiding areas with wolf urine, or reproductive investment, such as Siberian jays, *Perisoreus infaustus*, laying smaller clutches when exposed to predator calls (Eggers et al., 2006; Severud et al., 2011). Alarm calls can also contribute to the perception of long-term predation risk: resident little owls, *Athene noctua*, reduced their clutch size at sites where conspecific alarm calls were played, and migrant scops owls, *Otus scops*, avoided breeding at sites where owl alarm calls were presented (Parejo et al., 2012). Nonetheless, we currently understand so little about the importance of information about danger and interspecific

information networks in shaping the structure of communities that it is not possible to speculate on what the long-term ripple effects might be should the corridor of wary silence beneath a hunting hawk, bounded by the machine gun rattle of New Holland honeyeater alarm calls, one day expand into simply silence.

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